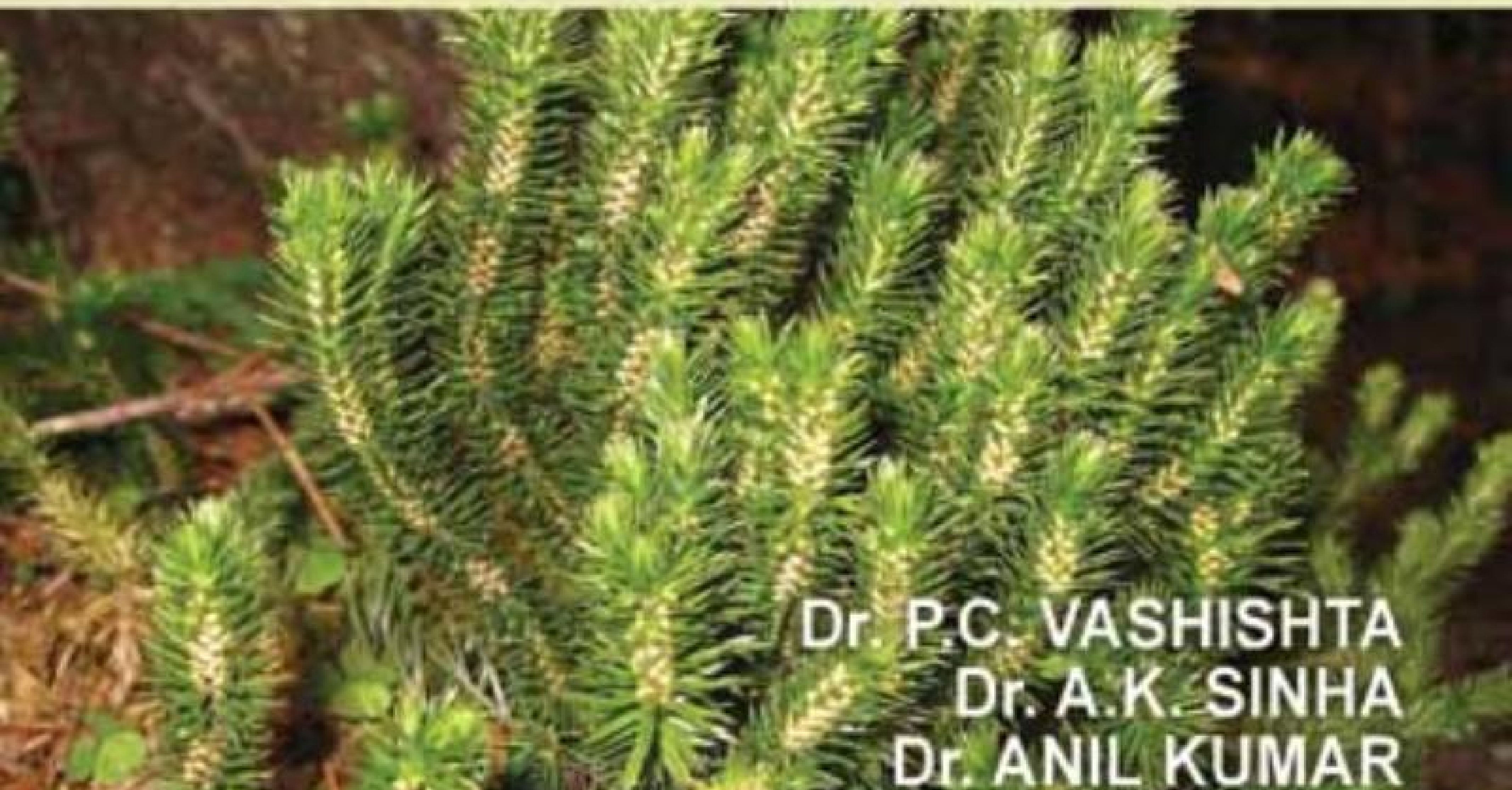
BOTANY
FOR DEGREE STUDENTS
PTERIDOPHYTA
(Vascular Cryptogams)



Dr. P.C. VASHISHTA
Dr. A.K. SINHA
Dr. ANIL KUMAR

S. CHAND

MULTICOLOUR ILLUSTRATIVE EDITION

Botany for Degree Students

Pteridophyta

(Vascular Cryptogams)

P.C. VASHISHTA
M.Sc.; Ph.D.; P.E.S.I. (Retd.)
Ex. Principal Govt. College, Sector-II
CHANDIGARH AND D.A.V. COLLEGE, HOSHIARPUR

Revised by

A.K. SINHA
M.Sc., Ph.D., F.P.S.I., F.S.B.
Reader & Head (Retd), Department of Botany,

Dr. ANIL KUMAR
M.Sc., Ph.D.
Department of Botany

Feroze Gandhi Post-Graduate College
(Kanpur University), RAE BARELI (U.P.)

S. CHAND & COMPANY LTD.
(AN ISO 9001 : 2000 COMPANY)
RAM NAGAR, NEW DELHI - 110055

S. CHAND & COMPANY LTD.
(An ISO 9001 : 2000 Company)
Head Office : 7361, RAM NAGAR, NEW DELHI - 110 055
Phones : 011-23672080-81-82; Fax : 91-11-23677446
Shop at: **schandgroup.com**
E-mail: **schand@vsnl.com**

- 1st Floor, Heritage, Near Gujarat Vidhyapeeth, Ashram Road, **Ahmedabad**-380 014. Ph. 27541965, 27542369, ahmedabad@schandgroup.com
- No. 6, Ahuja Chambers, 1st Cross, Kumara Krupa Road, **Bangalore**-560 001. Ph : 22268048, 22354008, bangalore@schandgroup.com
- 238-A M.P. Nagar, Zone 1, **Bhopal** - 462 011. Ph : 4274723. bhopal@schandgroup.com
- 152, Anna Salai, **Chennai**-600 002. Ph : 28460026, chennai@schandgroup.com
- S.C.O. 6, 7 & 8, Sector 9D, **Chandigarh**-160017, Ph-2749376, 2749377, chandigarh@schandgroup.com
- 1st Floor, Bhartia Tower, Badambadi, **Cuttack**-753 009, Ph-2332580; 2332581, cuttack@schandgroup.com
- 1st Floor, 52-A, Rajpur Road, **Dehradun**-248 001. Ph : 2740889, 2740861, dehradun@schandgroup.com
- Pan Bazar, **Guwahati**-781 001. Ph : 2514155, guwahati@schandgroup.com
- Sultan Bazar, **Hyderabad**-500 195. Ph : 24651135, 24744815, hyderabad@schandgroup.com
- Mai Hiran Gate, **Jalandhar** - 144008 , Ph. 2401630, jalandhar@schandgroup.com
- A-14 Janta Store Shopping Complex, University Marg, Bapu Nagar, **Jaipur** - 302 015, **Phone : 2709153**, jaipur@schandgroup.com
- 613-7, M.G. Road, Ernakulam, **Kochi**-682 035. Ph : 2381740, cochin@schandgroup.com
- 285/J, Bipin Bihari Ganguli Street, **Kolkata**-700 012. Ph : 22367459, 22373914, kolkata@schandgroup.com
- Mahabeer Market, 25 Gwynne Road, Aminabad, **Lucknow**-226 018. Ph : 2626801, 2284815, lucknow@schandgroup.com
- Blackie House, 103/5, Walchand Hirachand Marg , Opp. G.P.O., **Mumbai**-400 001. Ph : 22690881, 22610885, mumbai@schandgroup.com
- Karnal Bag, Model Mill Chowk, Umrer Road, **Nagpur**-440 032 Ph : 2723901, 2777666 nagpur@schandgroup.com
- 104, Citicentre Ashok, Govind Mitra Road, **Patna**-800 004. Ph : 2300489, 2302100, patna@schandgroup.com

© 1971, P.C. Vashishta

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior permission of the Publishers.

First Edition 1971
Subsequent Editions and Reprints 1972, 73, 74, 75, 77, 80, 82, 83, 84
86, 87, 88, 90, 91, 92, 93, 95, 96, 97, 99, 2000, 2001, 2003
Revised Edition 2005

First Multicolour Illustrative Revised Edition 2006

Code: 03 353
ISBN : 81-219-2785-4

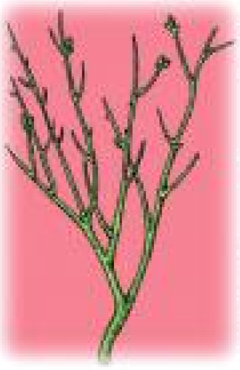
PRINTED IN INDIA
By Rajendra Ravindra Printers (Pvt.) Ltd., 7361, Ram Nagar, New Delhi-110 055
and published by S. Chand & Company Ltd. 7361, Ram Nagar, New Delhi-110 055

Contents

1. The Vascular Cryptogams (Pteridophyta) ... 1—56

Introduction; Characteristic features; Habitat of Pteridophytes; Alternation of Generations; Interpolation or Antithetic Theory; Homologous or Transformation Theory; Modern Concept; Cytology and Artificial Induction of Apospory; Origin of the Vascular Cryptogams; Anthocerotean Theory; Protocorm Theory; Phyton Theory; Evolution of the Sporophyte; Telome Theory; Fossil Record and Geological time scale; Coal formation; Classification.

2. Division–Psilophyta Class–Psilophytopsida ... 57—77



Classification; *Rhynia major*; Discussion; Anatomy; Spore Bearing Members.

3. Division–Psilophyta Class–Psilotopsida ... 78—111

Psilotum; Vascular Region; Anatomy of the Leaf; Sporangia; Morphology of the Sporangium; Gametophyte Generation; Mature Prothallus; Sexual Reproduction; The Embryo; *Tmesipteris;* Vascular Region; Morphology of the Sporangial Stalk; Embryogeny; Chromosome Number; Affinities of Psilotales.

4. Lycophyta–Eligulopsida ...112—153

Classification; *Lycopodium* Linn; Distribution and Occurrence; Growth; Anatomy; Leaf; Root; Vegetative Propagation; Organisation of the Strobilus; Sporangium; Structure of the Sporangium; Dehiscence of Sporangium; Gametophyte; Structure of the Spore; Germination of the Spore; Structure of Mature Prothallus; Sex Organs; Antheridia; Structure of Mature Antheridium; Archegonia; The Embryo; *Lycopodium selago* and *L. phlegmaria*; *L. clavatum* and *L. annotinum*; *L. cernuum* and *L. inundatum*; Deviations from Normal Life cycle; Economic Importance; Chromosome Number; *Phylloglossum* Kunze; Anatomy; Gametophyte; Embryo.

5. **Lycophyta–Ligulopsida** ...154—180

Isoetales; *Isoetes* Linn; Axis; Growth; Root; Leaf; Anatomy; Leaf; Reproduction; The Velum; Sporangia; Gametophytes; Microgametophyte; Archegonia; The embryo.

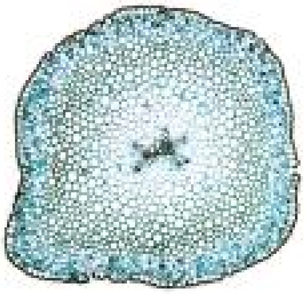
6. **Lycophyta–Ligulopsida (Contd.)** ...181—219

Selaginellales; Morphology of the Sporophyte; Organization of the Strobilus Anatomy; Reproduction. The Gametophytic Generation; The Embryo; Heterospory.

7. **Sphenophyta (Benson, 1957)** ...220—254

Equisetaceae; *Equisetum* Linn; The Sporophyte; Vegetative Propagation; Gametophyte; Anatomy of the Prothallus; Sex Organs.

8. **Filicophyta or Pterophyta** ... 255—338



Vegetative Propagation; Stelar System in Vascular Cryptogams; Spore Producing Members; Prothallus; The Sex Organs; Embryology, Classification.

9. **Eusporangiopsida Ophioglossales** ... 339—383

Ophioglossum L.; Anatomy, Reproduction; Gametophytic Generation; Embryogeny, Taxonomic Position; Sporangium; Gametophytic Generation; Embryology.

10. **Eusporangiopsida (Contd.)–Marattiales** ... 384—398

Characteristic Features; Family Marattiaceae, Genus *Marattia* Swartz; Sporophyte; Gametophyte; Embryogeny.

11. **Protoleptosporangiopsida** ... 399—415

Genus *Osmunda* L.; Anatomy, Reproduction, Sporangia; Gametophytic Generation, Sexorgans; Archegonium; Embryogeny.

12. Leptosporangiopsida ... **416—429**

Family : Schizaeceae; Discussion.

13. Family Gleicheniaceae Genus *Gleichenia* ... **430—444**

Gleichenia Smith; Soporophyte; Anatomy, Reproduction, Gametophyte; Embryogeny.

14. Family Polypodiaceae Subfamily Drypteridioideae ... **445—464**

Introduction, Genus *Dryopteris*; Sporophyte; Reproduction; Gemetophyte Generation.

15. Family Polypodiaceae Subfamily Pteridoideae ... **465—480**

Genus *Pteridium aquilinum* (L. *Kuhn*); Sporophyte; Genus *Pteris* Linn;

16. Family Polypodiaceae Subfamily Polypodioideae ... **481—499**

General Characteristics; Genus *Polypodium* L.; Reproduction; Genus *Adiantum* L.; Morphology; Anatomy; Spore Producing Members; Gametophyte.

17. Hymenophyllaceae ... **500—522**

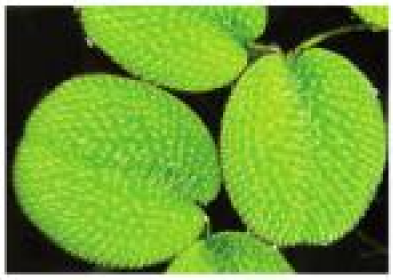
Family : Hymenophyllaceae; Matoniaceae; Cyatheaceae; Dicksoniaceae.

18. Pterophyta—Leptosporangiopsida—Marsileales ... **523—564**

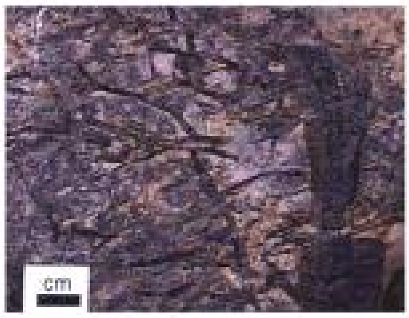
Marsilea L.; Sporophyte; Anatomy, Reproduction; Spore, Formation; Sporangia; Gametophyte Generation; Embryogeny; *Regnellidium*, Linn; *Pilularia*, Discussion.

19. Pterophyta– Leptosporangiopsida–Salviniales ... 565—585

Salvinia Guettard; Sporophyte Generation; Gametophyte Generation; *Azolla* Lamarck; Anatomy; Reproduction; Megagametophyte; Embryogeny.



20. General Discussion ... 586—605



Fossil Lycopods; Fossil Sphenophytes, ; Biotechnology, Tissue culture of Pteridophytes; Economic Important of Pteridophytes; Diversity and Distribution of Pteridophytes in India.

Bibliography ... 607—620

Reference Books ... 621—622

Index ... 623—628

SELAGINELLA
FERTILE SPIKES

CHAPTER 1

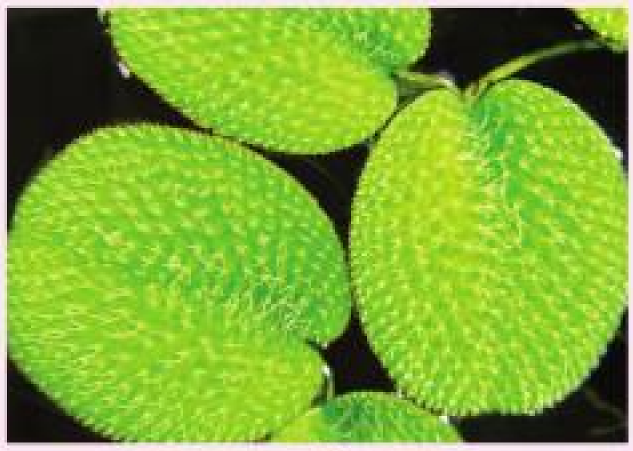
The Vascular Cryptogams (Pteridophyta)

- Introduction
- Characteristic features
- Habitat of Pteridophytes
- Alternation of generations
- Abnormalties in the life cycle (Apogamy, Apospory)
- Origin of the vascular cryptogams
- Evolution of sporophyte
- Fossil record and geological time scale
- Classification
- Pteridology in India

Introduction

The word cryptogams is a synthesis of two Greek terms ***kruptos*** meaning '***hidden***' and ***gamos*** meaning '***wedded***'. This single term encompasses all plants that reproduce by means of spores and, do not produce seeds. The algae, fungi, bryophytes and pteridophytes are all cryptogams. The pteridophyta are treated as vascular cryptogams as they have a well developed conducting system. They form the subject-matter of this book. The lower cryptogams (algae, fungi and bryophyta) have no conducting system. The term pteridophyta also has a Greek origin. ***Pteron*** means a "feather" and the name was originally given to this group because of their pinnate or feather-like fronds. ***Vascular cryptogams are, therefore, an assemblage of seedless vascular plants that have successfully invaded the land and reproduce by means of spores***.

The Pteridophytes formed a dominant part of earth's vegetation in the historic past (Two hundred eighty to two hundred thirty million years ago). In the present day flora, excluding the non-vascular plants, they rank only next to the spermatophytes. Although they have been largely replaced by the spermatophytes in the modern day flora, yet they occupy an important and a crucial central position in the evolutionary history of the plant kingdom. No doubt lesser in number, the pteridophytes lend a distinct charm and physiognomy to the landscape. The elegant tree ferns of the warm humid forests of eastern Himalayas, Pachmahri and Nilgiri hills, the epiphytic ferns and the hanging club-mosses of the tropical forests attract ones attention. The lithophytic and terrestrial forms that grow in comparatively larger numbers are also a source of great attraction because of their beautiful foliage. Some of them (about a dozen species) grow in water and form a luxuriant hydrophytic component of the lakes (***Salvinia***), ponds and pools (***Azolla***, ***Marsilea***). In India about five hundred species of fern allies have been reported. Dixit (1984) has raised the number to one thousand.



Salvinia

Azolla

The Pteridophyta have a long fossil history. Their first traces were recognised in the Silurian period of the late Paleozoic age (about 400 million years ago). They flourished well during Devonian, Mississippian and Pensylvanian periods of the late Paleozoic. ***Late Paleozoic can easily be regarded as the "Age of Pteridophyta."*** The tree ferns, giant horsetails and arborescent lycopods dominated the swampy landscapes of those ancient ages. The present-day lycopods (***Lycopodium***, ***Isoetes***, ***Selaginella***, ***Phylloglossum***) and Sphenopsids (***Equisetales***) are the mere relicts of the mighty lycopsid and sphenopsid group which once boasted of 120-foot ***Lepidodendron***, ***Sigillaria***, and the colossal ***Calamites.*** Only the present-day ferns have somehow managed to conserve the former stature, diversity and glory of their ancestors. ***Psilotum*** and ***Tmesipteris***, our two surviving remnants of ***Psilopsids*** retain the primitive features of the first land plants.

Lycopodium

Isoetes

Surange (1966) has given a detailed and a comprehensive account of the Indian fossil pteridophytes. He has described one fossil member of Psilophyta, seven of Lycopodiophyta, twelve of Arthrophyta and sixty six of Pterophyta. He has observed that the Indian Paleozoic and Mesozoic pteridophytes resemble quite closely those described from far flung areas of the southern hemisphere. A number of fossil ferns have been described from the Rajmahal hills in Bihar. Bose and Sah (1967) and Sharma (1969, 1971, 1972, 1973) have explored these hills and described as many as eighteen species of ferns and one of ***Selaginellites*** from Brindaban and Dhokuti areas. Suthar and Sharma (1986) presented a complete restoration of ***Solenostelopteris jurassica*** of Schizaeaceae from the jurassic flora of Rajmahal hills. They described the anatomical details of different organs. Sharma, Suthar and Bohra (1986) have given a detailed account of the work done on Indian fossil pteridophytes (Lycopods, Sphenopsids and ferns). They have pointed that pteridophytes occur throughout the Gondwana system but more frequently during Mesozoic era and the ferns make the major bulk of the assemblage. The Sphenopsida played an important role in the constitution of Glossopteris flora during the Palaeozoic whereas the Lycopods never played any significant role in the constitution of Indian fossil flora.

Characteristic Features

(*a*) Sporophyte

The vascular cryptogams possess an independent sporophyte with a vascular system. It exhibits a great variation in form, size and structure. All the living pteridophytes are nearly herbaceous except a few woody tree ferns. They may be dorsiventral or radial in symmetry and have dichotomously or laterally branched stems that bear microphyllous or megaphyllous leaves. The roots are generally adventitious, the primary embryonic root being short lived.

The stem, root and the leaves grow by means of a single, two-sided or three-sided apical cell or by a plurality of such apical initials. A distinct apical meristem has been reported in a number of **Lycophyta** (***Lycopodium***, ***Isoetes***). Bhambie and Puri (1985) recognised three different configurations of shoot apical meristems as : (***i***) a single conspicuous pyramidal apical cell and its nearby derivatives, (***ii***) a group of conspicuous pyramidal or cubical apical initials surrounded by smaller cells and (***iii***) a lump of meristematic tissue having a central zone and capped by an outer layer. In roots, four kinds of apical organisations have been recognised: (***i***) a single conspicuous pyramidal cell, (***ii***) a gradation from one to several cubical cells, (***iii***) a group of inconspicuous initials and (***iv***) four tiers of initials. Bir, S. S. and Randhawa (1984, 1987) studied the apical organisation in rhizome, root and leaf of twelve different ferns belonging to different groups and pointed out that a single apical cell always occupies the tip of each growing organ. This single apical cell is replaced by a group of initial cells when the shoot apex becomes sufficiently grown up and well developed. They supported the classical concept of a single apical cell in ferns. The vasculature of the sporophyte may be a simple protostele, medullated protostele (siphonostele), dictyostele, or a polycyclic stelar organisation. Vessels are also present in some members (***Selaginella***, ***Equisetum***). Loyal and Singh (1978) recorded the presence

Equisetum

image
not
available

12. Water is essential for fertilization. Diploid zygote is formed following fertilization.
13. Zygote develops into sporophytic plant body.
14. Alternation of Generation is an essential part of life cycle and is heterologous.

Habitat of Pteridophytes

Pteridophytes—the first land vascular plants, are represented by about 10,000 species distributed throughout the world, both in tropical and temperate climates. Most of the members of this group are terrestrial in nature, prefer to grow in cool and shady places, however aquatic and xerophytic habitat is not uncommon for pteridophytes. A short description of habitat of pteridophytes can be discussed as follows:

(*a*) Terrestrial habitat

Members right from fossil pteridophytes (***Rhynia sp.***) to most advanced pteridophytes (***Pteridium***) grow in terrestrial habitats. Among Psilophyta, terrestrial species are represented by ***P. nudum***, ***Osmunda sp***., ***Ophioglossum sp***. etc. Lycopods growing in such habits are ***L. clavatum***, ***L.cernuum***, ***L lucidum***, ***L. reflexum***, ***L.annotinum.*** Plants of ***Lycopodium*** are either creepers (***L. cernuum***), climbers (***L. volubile***) or mostly epiphytic in nature (***L. phlegmaria***, ***L.carinatum***). Most of the common species of ***Selaginella*** (***S. chrysocaulos***, ***S. kraussiana***, ***S. selagiuoides***), ***Isoetes*** (***I. coromandelina***) are terrestrial. Similar habitat is preferred by ***Equisetum*** sps, though its species ***E. debile*** can grow in hydrophytic, mesophytic as well as in xerophytic habitats. ***E***. ***palustris prefers swampy habitats. E. arvense*** grow in open grasslands, railway embankments and exposed sandy and dry places.

Osmunda

Ophioglossum

Most of the ferns are terrestrial in nature, mostly grow in hilly regions (***Dryopteris***, ***Pteris***, ***Pteridium***, ***Adiantum*** etc.) prefering moist and shady environment.

(*b*) Aquatic Pteridophytes

Most of the members of family Marsileaceae and Salviniaceae grow in aquatic and semi-aquatic habitats. Plants of these groups are commonly known as aquatic ferns. Few examples of aquatic pteridophytes ***are M. minuta***, ***M. quadrifolia***, ***Salvinia natans***, ***S. auriculata***, ***Azolla filiculoides***, ***A. microphylla*** and ***A. mexicana***. ***Two species of Isoetes*** eg. ***Isoetes englemanni*** and ***I. Japonica*** are semi-aquatic pteridophytes. ***I. panchananii***, a very common plant of Pachmarhi is also considered as plant of amphibious habitat.

(*c*) Xerophytic Pteridophytes

Most of the xerophytic plants are reported from the genus ***Selaginella.*** Some common Indian xerophytic species of ***Selaginella*** are ***S. wightii*** and ***S. repanda***. ***S. lepidophylla*** is another xerophytic plant. ***Marsilea condensata*** and ***M. rajasthanesis*** are xerophytic pteridophytes as well.

seasons and extensive dew). Under such circumstances these early land plants could not depend entirely upon the sexual process for propagation and had to adopt another method. This was accomplished by the development of zygote into embryo and ultimately into a diploid individual called the **sporophyte**. Development of the sporophyte involved certain changes that can be listed below :—

(*i*) Development of jacketed sex organs especially the archegonium.

(*ii*) The retention of the fertilised egg within the archegonium that could provide it with sufficient food.

(*iii*) The zygote or the fertilised egg divided mitotically and not meiotically to form a diploid embryo, which in primitive land plants distinguished into a sterile jacket enclosing a number of diploid cells or spore mother cells.

(*iv*) The diploid spore mother cells underwent meiosis to form tetrads of haploid spores. Such a primitive sporophyte is exemplified by ***Riccia***.

(*v*) Gradually the primitive sporophytes underwent progressive sterilisation and gave rise to complex sporophytes of liverworts like ***Marchantia***, ***Anthoceros*** and ***Mosses***. These sporophytes were dependent wholly or partially upon the gametophytes for food.

(*vi*) Enhanced sterilisation of the sporophyte led to the development of an independent sporophyte that developed vascular tissue and possessed root, stem and leaves. These sporophytes also bore sporangia that produced spores and disseminated them efficiently.

Marchantia

The events of apogamy and apospory were dismissed by Bower as 'ex post facto' events. He stated, "They illustrate the potentialites of plants of present day rather than evolutionary features of the remote past, and will have no part in producing that normal alternation which is characteristic of the Archegoniatae."

Homologous or Transformation Theory

This theory was put forth by Pringsheim (1876-77) and has a large number of supporters. Stebbins (1960) has also supported it. The proponents of this theory claim that the sporophyte is a modification of the gametophyte. They do not believe progressive sterilisation to be the cause of origin of photosynthetic tissues in the sporophyte. They do not regard the sporophyte and gametophyte individuals to be as different as postulated by the adherents of the antithetic theory. According to this theory the primitive land plants exhibited isomorphic alternations ***i.e.***, they had free living sporophytes and gametophytes that resembled each other in all respects except their genetic constitution and functions. They derived support from the following events :

1. Existence of isomorphic alternation of generations in the algae ***e.g.***, ***Cladophora***, ***Ulva***, ***Ectocarpus*** and ***Dictyota***. Both the generations are photosynthetic.
2. Presence of Chloroplasts in the sporophytes of some bryophytes.
3. Presence of tracheids in the gametophytes of some lower cryptogams ***e.g.***, ***Psilotum***.
4. Occurrence of phenomenon of apospory and apogamy. These deviations from the normal life cycle suggest that either generation can arise as an outgrowth from the other. These phenomena lend support to the view that sporophyte can be a modification of the gametophyte.

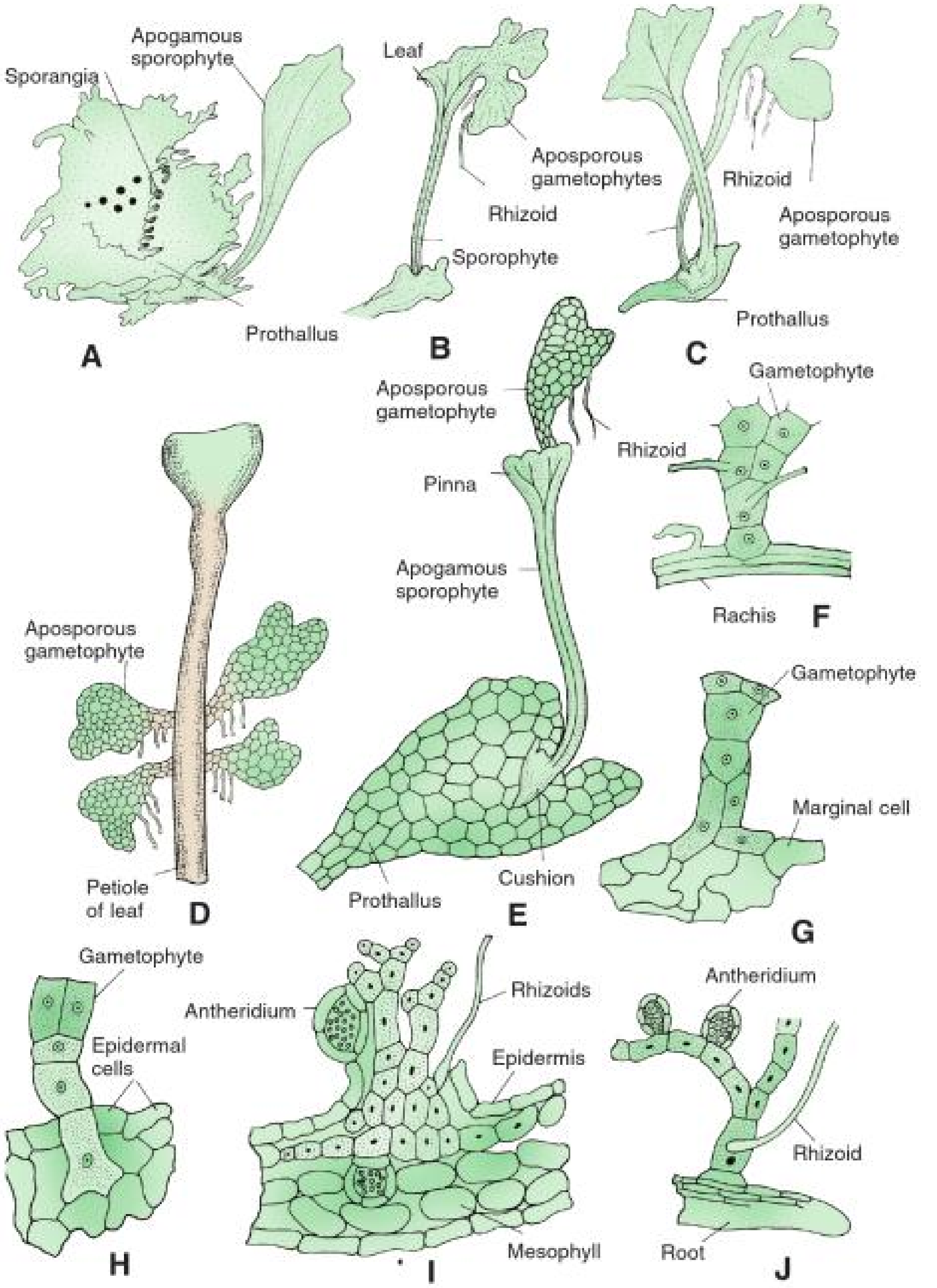

Apogamous sporophyte
Sporangia
Prothallus
A
Leaf
Aposporous gametophytes
Rhizoid
Sporophyte
B
Rhizoid
Aposporous gametophyte
Prothallus
C
Aposporous gametophyte
Rhizoid
Pinna
Apogamous sporophyte
Prothallus
Cushion
E
Aposporous gametophyte
Petiole of leaf
D
Gametophyte
Rhizoid
Rachis
F
Gametophyte
Marginal cell
G
Gametophyte
Epidermal cells
H
Antheridium
Rhizoids
Epidermis
Mesophyll
I
Antheridium
Rhizoid
Root
J

Fig. 1.2 (A–J). Apogamy and Apospory in ferns. **A.** Apogamous sporophyte arising from the gametophyte of ***Phyllitis scolopendrium*** (After Lang) ; **B–C.** Aposporous gametophytes arising from the primary leaves of sporophytes of ***Osmunda regalis*** (After Lang) ; **D.** Aposporous gametophytes arising from the petiole of ***Pteris vittata*** (After Palta) ; **E.** Apogamously produced sporophyte of ***P. vittata*** bearing aposporous gametophyte (After Palta) ; F–J Aposporous gametophytes of ***Pteridium aquilinum*** var. ***latiusculum*** ; **F.** Prothallus arising from epidermis of petiole; **G.** Prothallus arising from marginal cells of a pinna; **H.** Prothallus arising from leaf epidermal cells; **I.** Prothallus arising from mesophyll cell of pinna ; J. Prothallus arising from root epidermis. (F–J. After Takahashi, 1962).

intervention of spores. Bower reported it in two species of ***Trichomanes*** in 1885. In this case aposporous gametophytes were produced from soral regions of the leaf and from leaf tips. Later apospory was reported by several authors in many genera and species of ferns. Druery and Neurnberg (1938) and Steil (1939, 1951) reviewed the literature on apospory and apogamy in ferns. Bristow (1962) developed gametophytes from a callus tissue derived from the sporophyte of the fern ***Pteris cretica***. This callus developed into gametophytes when grown in media containing only mineral nutrients. De Maggio and Wetmore (1961) isolated zygotes and undeveloped embryos from the archegonia of ***Todea barbara*** and cultured them. They were able to induce these isolated zygotes to develop into thalloid structures that resembled the gametophytes of this fern. Bell (1959) reviewed many cases of apospory in ferns and was tempted to state that the phenomenon of apospory must be general among ferns. Wetmore and De Maggio (1963) have also reviewed cases of apospory and apogamy among ferns.

Cytology and Artificial Induction of Apospory

In ***Osmunda javanica*** Sarbadhikari (1936) reported the formation of gametophytes from any vegetative part of the young or old sporophyte. He observed filamentous as well as heartshaped prothalli arising from the sporophyte. These prothalli bore antheridia containing spermatozoids but did not produce archegonia. Later apogamous sporophytes also developed from these aposporously produced gametophytes. Lawton (1936) recorded the presence of both antheridia and archegonia on the aposporously produced gametophytes of ***Osmunda regalis*** and ***Cystopteris fragilis.*** The gametophytes were diploid and so were the sex organs and the gametes. As a result of normal fertilisation tetraploid embryos and sporophytes were produced. Such tetrapoloid sporophytes have been induced to produce tetraploid aposporous gametophytes. This may lead to the formation of octaploid sporophytes. Lawton also observed cases where the diploid gametes of diploid aposporus gametophytes cross fertilise with haploid gametes from haploid gametophyte and produce triploid sporophytes. Lawton (1932) also induced apospory in ***Aspidium marginale*** and ***Woodwardia virginica*** and produced tetraploid sporophytes. Manton (1932) induced apospory in ***Osmunda regalis*** and produced diploid, triploid and tetraploid gametophytes and sporophytes.

Cystopteris

Tectaria trifoliata

W.N. Steil (1944) induced the formation of aposporous gametophytes on the young leaves of apogamously produced sporophytes of ***Tectaria trifoliata.*** He was able to induce the formation of gametophytes from the margins of the young leaves and from the hair borne on the petiole of the first formed leaf of the sporophyte. In both the cases the gametophytes were produced in large numbers.

Goebel (1907) and Palta (1973) induced the formation of prothalli from the petiole and laminar surface of the pinnae in ***Pteris vittata*** (Fig. 1.2, D). Goebel also observed the formation of thalloid structures bearing antheridia, rhizoids, stomata, and even vascular strands on the detached juvenile leaves of ***Alsophila van-geertii*** and ***Ceratopteris thalictroides***. These thalloid structures resembled gametophytes in possessing antheridia and rhizoids and sporophytes in possessing stomata and vascular strands. He designated them as "Mittelbildungen".

Parthenogenesis

Selaginella

This may be defined as ***the phenomenon where the egg develops into embryo without the act of fertilisation.*** This act is very common in algae, fungi and ferns. According to Farmer and Digby (1907) in homosporous leptosporangiate ferns, apospory was followed by neither apogamy nor fertilisation but by parthenogenesis. There are various species of ***Selaginella*** where parthenogenesis have been reported. In ***S. atroviridis*** with unisporangiata strobili the egg develops into embryo without fertilization. This phenomenon has also been observed in ***S. intermedia*** and ***S. langere*** (Hieronymus, 1911). Bruchman (1912, 1919) and Goebel (1915) observed parthenogenesis in a few other species of ***Selaginella*** with bisporangiate strobili (***S. anacardia***, ***S. rubicaelis*** and ***S. helvetica***). In these cases archegonial neck remains closed and does not permit spermatozoids to enter. The egg, in these species develops directly into embryo. In ***Marsilea drummondii*** too the megaspores on germination produced diploid megagametophyte (1970 Strasburger), which without fertilization developed into sporophytes.

ORIGIN OF THE VASCULAR CRYPTOGAMS

A number of theories have been put forward to explain the origin of the vascular cryptogams. All of them tend to explain the origin of the independent sporophyte and are based on two assumptions :

1. The vascular cryptogams originated from the bryophytes. Bower (1935), Lignier (1903), and Zimmermann (1930, 1938) regard Bryophytes and Pteridopytes as two divergent lines originating from a hypothetical group of archegoniate land plants. Campbell (1895) and Smith (1958) believed them to have originated from an anthocerotean type of a bryophyte.
2. The adherents of the second view believe algae to be the ancestors of the vascular cryptogams. The proponents of this idea trace the origin of the pteridophytes from various algal groups. Scott (1900), Bohlin (1901), Lotsy (1909), Church (1919), Fritsch (1916, 1945), Eames (1936), Arnold (1947), Gregus (1955), Andrews (1956), Axelrod (1959) and Mehra (1968) are the chief proponents of the idea of algal origin of the pteridophytes.

Anthocerotean Theory

It was put forth by Campbell (1859) and later supported by Smith (1938). Presence of intercalary meristem and photosynthetic tissue in the sporophyte of ***Anthoceros*** lead Campbell (1895, 1899) to put forth the view that such sporophytes are very near to the independent sporophytes of the vascular cryptogams. He conjectured, "Were the foot of the sporophytes in ***Anthoceros*** prolonged into a root penetrating the earth, it would become quite independent of the gametophyte, and were a special assimilative organ or leaf developed, a condition directly comparable to the sporophyte of the lower Pteridophytes or ferns would result". The discovery of the rootless, leafless and dichotomously branched psilophytales led Smith (1938) to advance his views favouring Campbell's views. Smith followed the origin of vascular cryptogams from ***Anthoceros***-like ancestors along the following assumptions :

(*i*) The intercalary meristem of ***Anthoceros***-like sporophytes shifted to the apex and initiated dichotomous branching (Fig. 1.4., A—D).

to the fossil evidence. He imagined the transmigration to have taken place at a time much earlier than the Devonian. Church postulated the origin of land plants from a hypothetical or imaginary group of marine algae which he called as **Thalassiophyta.** The Thalassiophyta were assumed to have originated along several independent lines from the flagellated green algae. While giving a description of the process of the transmigration, Church (1919) imagined a universal ocean covering the entire face of the earth. He supposed this ocean to the inhabited with a countless number of minute and free swimming organisms. This stage was called the **Plankton stage.** Later the sea bottom started rising at certain places and the plankton stage was succeeded by the **'Benthic Stage,'** which included a number of attached and rooted sea weeds. This process went on for ages and the attached sea weeds gradually attained a very high degree of organisation. This uplift of sea bottom was accompanied by a large number of environmental changes that included increase in the amount of atmospheric oxygen and light intensity. The uprising sea bottom later emerged out of the sea and that was the first sight of land. This brought in the conditions of desiccation and insolation. The sea weeds which emerged out of water along with the land were now under terrestrial environments and were exposed to free oxygen, light and desiccation. This led to struggle for existence among the exposed algae and brought in adaptations among them. Natural selection played its role and more adapted changes accompanied by variations were brought about in these sea weeds. Church believed that land plants originated under tropical conditions. Under the changed set up of environments the exposed and terrestrial sea weeds attained a high degree of complexity and had exhibited differentiation into stem and leaves. Roots appeared in the form of holdfasts. Conducting strands in the form of phloem elements had already appeared. These sea weeds possessed heteromorphic alternation of generations. When the transmigration had occurred these highly organised plants merely required to become adapted to subaerial environments. These included the appearance of xylem elements and stomata to permit a ready stream of transpiration. The roots which hitherto served the only function of attachement were required to take on a new function of absorption. The spores needed a resistant cell wall to equip them for the changes and chances of dissemination by air. According to Church the sporangial tetrads of the early vascular plants originated from the unilocular tetrasporangia of the algal ancestors. The female sex organs or the archegonia were postulated to have evolved independently along various lines. Both the gametophytes and the sporophytes were believed to be already leafy and autophytic. It appears from the above description that brown algae were considered to be the probable ancestors of the land plants.

The geologists do not regard the land to have emerged from the sea. They believe that land was already in existence when the oceans appeared. Church's hypothesis, therefore, is not considered to be tenable. Moreover, it has been urged that the highly organised transmigrant brown algae that were used to marine environment were too specialised to adapt entirely to new mode of existence on dry land.

2. Greguss's Hypothesis

Greguss put forth his views in 1955. He traced the origin of vascular plants from the three major divisions of algae, ***i.e.***, Chlorophyta, Phaeophyta and Rhodophyta. He did not take into consideration the pigment constitution, the products of photosynthesis, and the presence or absence of cilia in the reproductive units. He laid stress on the branching of the organisms ***i.e.***, whether it is dichotomous, monopodial or verticillate. He derived mosses from Chlorophyceae and liverworts from the Phaeophyceae. In the same way he traced the origin of the ***Rhynia*** and ***Horneophyton*** from the Chlorophyceae and ***Psilotum*** and ***Tmesipteris*** from the Phaeophyceae. Lam (1957) criticised Greguss's hypothesis and regarded it as based on unsound footings. He almost disregarded the phylogenetic relationship of the plant groups while tracing their origin ***e.g.***, Psilophytales and Psilotales that are quite closely related to each other have been regarded as descendants of two different algal groups.

some mosses). These sex organs were projecting type, superficial and jacketed. The sporophytes were independent and their terminal ends were sporiferous, ***i.e.***, the sporangia were terminal and had a distinct sporangial wall. These developments gave rise to a **terminal sporangiate archegoniate plexus** (plants). In these plants the archegonia after fertilization retained the oospore. The independent sporophytes of this plexus followed two lines of development:

(*a*) Along one line the sporophytes, developing from the oospores enclosed within the archegonia, did not become free and remained attached to the gametophyte, ***i.e.*** they became dependent upon the gametophyte. The gametophytes of this line of evolution followed two courses of development. Along one line the sex organs did not become embedded, whereas along the other line the sex organs became embedded. The sporophytes with the former type of gametophytes gave rise to the liverworts and the mosses, whereas those of the other type gave rise to the Anthocerotae. Both the lines of evolution ended blindly. The spermatozoids were biciliate.

(*b*) This line of evolution led to the appearance of vascular tissues in the sporophytes which remained independent and became well established to life on land. The gametophytes had embedded sex organs with multiflagellate spermatozoids. The sporophytes, however, bore terminal sporangia and were mostly dichotomously branched. This led to the appearance of the **Rhyniaceous Stock.** This stock fanned out into the following four lines of evolution :

(*i*) **Prosphenopsid line :** It was linked with the Rhyniaceous stock by plants like ***Protohyenia***, which gave rise to ***Hyenia*** and ***Calamophyton*** of the early and middle Devonian periods. From them arose the Sphenophyta (Equisetales).

(*ii*) **Pro-pteropsid line :** It was linked with the Rhyniaceous stock through ***Protopteridum*** like plants. They had terminal sporangia but also bore short, sterile branches with **Circinate ptyxis.** Such plants gave rise to the Filicales or Filicophyta.

Hyenia and *Calamophyton*

(*iii*) **Progymnospermopsid line :** It is represented by ***Archaeopteris***, ***Callixylon*** type of plants that showed secondary growth. Some of them had also established heterospory. They gave rise to the pteridosperms on the one hand and to Gnetophyta, Cordaitales, Coniferales and Ginkgoates along other independent lines of evolution. The Pteridosperms gave rise to the Bennettitales and the Cycadales.

(*iv*) **Psilophytaceous line.** It bifurcated into two lines of evolution. One culminated in ***Rhyniaceae*** whereas the other gave rise to the Psilotales represented in the modern flora by ***Psilotum*** and ***Tmesipteris.***

(B) Lycopodiaceous Line of Evolution

It started directly from the proto-archegoniatae. The sporophytes remained free and developed vascular system and lateral sporangia as specified by ***Baragwanathia*** and ***Drepanophycus.*** The gametophytes developed embedded sex organs with biciliate spermatozoids. This line was termed by Prof. Mehra as **Lateral sporangiate plexus.** From this plexus arose the pro-lycopsida represented by ***Baragwanathia*** and ***Drepanophycus.*** From this pro-lycopsid stock there fanned out the various orders to the lycophyta, ***e.g.***, the Lycopodiales, Selaginellales, Lepidodendrales and Isoetales through Pleuromiales.

These early land plants evolved into the higher vascular cryptogams along three independent lines of evolution. These were the Lycopsid, Sphenopsid and Pteropsid trends of evolution. During the course of this evolution certain **elementary processes** of progressive differentiation took place in the sporophytes. These can be listed as : (***i***) Overtopping (***ii***) Plantion, (***iii***) Webbing or syngenesis, (***iv***) reduction, and (***v***) recurvation. All these elementary processes of organogenesis were believed to have occurred in varying degrees in the different taxonomic groups. These will be discussed separately.

Overtopping

The equally dichotomising axes developed unequal dichotomy (Fig.1.5 A-B). This resulted in the formation of short and long branches. The short branches appeared as lateral shoots. This led to the development of a sympodial axis which ultimately changed to a monopodial axis with lateral branches. These lateral branches metamorphosed into leaves.

Planation

The equal dichotomies were originally in more than one plane. They were arranged in planes successively at right angles (Fig. 1.5, C). During the process of **planation** the dichotomies became arranged in a single plane. It is an important process that led to the evolution of the leaf.

Syngenesis or Webbing : (Fig. 1.5, D-E). As the name indicates the adjacent telomes and mesomes were connected with each other by the development of a parenchymatous tissue between them. This is also called parenchymatous webbing. During this process the steles of the concerned telomes also fused. Syngenesis was considered to be of two types by Zimmermann:-

(*a*) Foliar syngenesis

During this process there is coalescence or fusion of apical meristems of the telomes. When these meristems fuse to form a marginal meristem, a lamina with veins develops. The activity of these meristems leads to the formation of parenchymatous webs between the telomes. Such developments resulted in the formation of lateral foliar appendages. In case foliar syngenesis is accompanied by overtopping, the leaves with pinnate venation are formed. Sometimes foliar syngenesis is accompanied by fusion of the vascular strands. This results in the development of **netveined** leaves or leaves with reticulate venation. Overtopping, planation and foliar webbing brought about the evolution of a megaphyllous leaf.

(*b*) Axial syngenesis

Zimmermann visualised that during this process there was absorption of a number of branches into a single stout axis. The fusing branches had **protosteles** and their fusion led to the appearance of a complex stelar organisation. In case the shoots united by the formation of parenchymatous webs the resulting stelar organisation was a polystelic condition. In case during axial syngenesis the steles anastomosed in different manners, the resultant stelar organisation was of diverse types, ***e.g.***, siphonostele, eustele, solenostele.

Reduction

It is supposed to have brought about the evolution of simple and unbranched microphyllous leaves of the lycopods (***Lycopodium***, ***Selaginella***, ***Isoetes***). It was brought about by the reduction of the syntelome to a single needle-like lateral appendage (Fig. 1.6, **A-C**).

Recurving

During this process the fertile telomes were supposed to become reflexed (Fig. 1.6, **H, I**). As a result the sporangium assumes an inverted position. Zimmermann called this process as **incurvation.** Wilson (1953) recognised two processes —

4. Structure of archegonia–the female reproductive organ is fundamentally similar in both the groups.
5. In both a single ovum or egg cell is protected by a layer of sterile investing cells.
6. In pteridophytes too like the bryophytes, the antheridium,– the male reproductive organ usually consists of a single layered jacket enclosing a mass of androcytes or antherozoid mother cells.
7. Antherozoids are ciliated in both.
8. Presence of water in liquid state is necessary for fertilization.
9. Sexual Reproduction is of oogamous type.
10. Both the groups show clearly defined heteromorphic alternation of generation; with some exceptions.
11. Sporangia are multicellular and spore development is same in both the groups.

But the pteridophytes differ with Bryophytes in some respects. The points of differences are as follows :

1. Plant body is sporophyte in Pteridophytes whereas the adult plants is a gemetophyte in bryophytes.
2. Plant body of pteridophytes are differentiated into leaf, stem and root where as in Bryophytes the plantbody is thalloid in nature.
3. Sporophytes are nutritionally independent of gametophyte except for very short period during embryonic stage in case of Pteridophytes, however in Bryophytes sporophytic phase is totally dependent on gametophytes.
4. In Pteridophytes sporophytes are strengthened with well developed vascular organizations/ tissues whereas the Bryophytes are devoid of vascular tissues/organizations.

Pteridophytes and Gymnosperms

Pteridophytes are designated as first land vascular plants because its dominant sporophyte plant body possesses well developed conducting tissue system. The vascular tissues are composed of xylem, phloem and other mechanical elements required for conduction of water and food material. Though in this respect pteridophytes resemble the higher plants but for seed bearing capacity. Pteridophytes approach seed habit through its heterosporous species (***Selaginella***, ***Marselia*** etc). The points of resemblances and differences between Pteridophytes and Gymnosperms are as follows:

1. The gametophytic generation is camparatively reduced in case of Gymnosperms as it is completely dependent upon sporophyte, whereas in pteridophytes the gametophytic generation is partially independent.
2. Root system of Pteridophytes are camparatively less developed and primitive where as in Gymnosperms roots are much more developed and complex and provide better anchorage to plant for efficient use of soil nutrients.
3. Heterosporous pteridophytes resemble with Gymnosperms but spore germinate ***in situ***, whereas the megaspore is retained within megasporangium in case of Gymnosperms.
4. Secondary growth in Pteridophytes are normally absent, though unique type of secondary growth is reported in ***Isoetes***, ***Stylites*** and ***Botrychium***. In Gymnosperms Secondary Growth is common and prominent.

Botrychium

image
not
available

9. Siliceous Colloids

These are formed by the dissolution of siliceous shells of diatoms, radiolarians and sponges and are found at the bottom of the sea. Some organisms get embedded in this siliceous colloid and are preserved. In some cases even the flagella of some unicellular flagellates have been nicely preserved. Wetzel, Otto (1953) described a unicellular flagellate ***Ophiobolus utinensis*** from the Upper Cretaceous flints and chalks of Europe. In this case Wetzel was able to photograph even the flagella.

10. Actual Remains

Such plant fossils are of comparatively young age and do not decompose completely due to low temperature or vacuum. All materials that are resistant to natural decomposition are preserved like this, ***e.g.***, cuticle, cutin, sporopollinin in the walls of pollen grains and spores.

11. Chemical Remains

Chemical materials like amino acids and hydrocarbons may be obtained in a natural state or in a modified form from the rocks in which organic matter of the petrified plant part or organ has been incorporated.

12. Products of Activity of Organism

Sometimes products excreted by living organism are obtained from the excavations, ***e.g.*** secreted lime deposits of algae. Such products have been found on pottery and other manufactured goods discovered during excavations.

Pseudofossils

These are unreal fossils which appear like real ones and are not the actual remains of plants and animals. They resemble the leaves and stems of plants or the filaments of algae but in actual practice they are outright fakes or artifacts formed by the peculiar arrangement or deposition of the mineral particles in the crevices of rocks. One such fossil named as ***Dendrites*** resembles the fern leaves but on closer examination it was found to be nothing but mineral formations simulating a fern leaf.

Coal Formation

Coal is one of the major fuels in daily use. It is, in fact, the changed form of vegetation which was existing on this earth. Due to various earth movements thick forests at the past ages got buried inside the earth and the remarkable change in temperature and pressure conditions, thus produced, changed them into thick carbonaceous seams which we mine or sometimes quarry in the form of coal. The thickness of the coal seams varies from exposure to exposure.

Geologically speaking, the coal deposits of the world are divisible into two groups as follows:

1. Carboniferous coal, ***i.e.***, coal of carboniferous period of Palaeozoic era, produced about 220 to 275 million years ago.
2. Tertiary coal : It is comparatively quite younger, produced in nature 70 million years ago.

Based upon the percentage of carbon contents, coal has been classified into four parts as below:

1. Peat coal.
2. Lignite coal.
3. Bituminous coal.
4. Anthracite coal.

Anthracite coal is the most pure variety whereas Peat coal is poorest so far as the percentage of carbon contents is concerned.

Class Filicineae.

- (*i*) Order **Ophioglossales.**
- (*ii*) Order **Filicales.**
- (*iii*) Order **Osmundales.**
- (*iv*) Order **Marattiales.**
- (*v*) **Fossil orders.**

The increasing knowledge about the vascular anatomy and the position of sporangia in the above mentioned sub-divisions has revealed marked divergence among them from one another. The modern writers thus consider that the differences between the Psilopsida, Lycopsida, Sphenopsida and Pteropsida series are of the magnitude of a division. Smith (1955), Bold (1957), Benson (1957) and Zimmermann (1959) have given these groups the rank of a division. According to the recommendations of **I.C.B.N.** (1952) the name of the division should end in the suffix **phyta**, of a sub-division in **phytina** and of a class in **opsida.** On this basis Smith (1955) divides the vascular cryptogams into 4 divisions, **Psilophyta**, **Lepidophyta**, **Calamophyta** and **Pterophyta**. Some writers suggest other names. Given below with slight modifications is one of the widely accepted modern classifications of the vascular cryptogams :—

I. Division Psilophyta

In it are included the most primitive and oldest known land inhabiting vascular plants which are rootless. The division comprises the following classes :—

1. **Class Psilophytopsida.**
   - (*i*) Order **Psilophytales.** It includes the most primitive fossil vascular cryptogams e.g. ***Rhynia***, ***Horneophyton***, ***etc.***
2. **Class Psilotopsida.**
   - (*i*) Order **Psilotales**. It includes two living genera which are allied to the Psilophytales. These are ***Psilotum*** and ***Tmesipteris***.

II. Division Lycophyta or Lepidophyta

Bold used the term **Microphyllophyta** for this division. On the basis of the presence or absence of ligules, this division may be divided into the following two classes :—

1. **Class Eligulopsida.**
   - (*i*) Order **Lycopodiales**. The order includes **homosporous**, **non-ligulate**, forms such as ***Lycopodium*** and ***Phylloglossum.***
2. **Class Ligulopsida**. The class includes **heterosporous** froms with **ligulate leaves**. The four orders recognisable in this class are :—
   - (*i*) Order **Selaginellales** represented by ***Selaginella.***
   - (*ii*) Order **Isoetales** represented by ***Isoetes.***
   - (*iii*) Order **Pleuromeiales**. e.g. ***Pleuromeia***.
   - (*iv*) Order **Lepidodendrales** represented by ***Lepidodendron***, ***Stigmaria***, ***Lepidocarpon***.

III. Division Arthrophyta or Calamophyta or Sphenophyta

The division includes two classes :—

1. **Class Sphenophyllopsida.** This class includes the well-known extinct genus **Sphenophyllum** which is placed in the following order:—
   - (*i*) Order **Sphenophyllales.**

According to Parihar (1996) the classification system of Pteridophytes has undergone vast changes during the last five decades and modern system of classification divides Pteridophytes into seven divisions as : Rhyniophyta, Trimerophytophyta, Zosterophyllophyta,Psilotophyta, Lycopodiophyta, Equisetophyta and Polypodiophyta. It was Bold (1973) who has differentiated Psilophytes into living and fossil groups. The living Psilophytes were placed under division Psilotophyta and extinct psilophytes were divided into three divisions ***i.e*** Rhyniophyta, Trimerophytophyta and Zosterophyllophyta. Taylor (1981) followed almost the similar pattern and proposed three divisions as Rhyniophyta, Zosterophyllophyta and Trimerophyta for early vascular plants.

The *characteristic features* of seven new divisions of Pteridophyta are described below :

(*i*) Rhyniophyta : Rootless plant body which was differentiated into two parts : an under ground rhizome which bear rhizoids and an errect aerial leafless portion arising from underground rhizome; aerial branches were dichotomously branched, some of which bear terminal sporangia. Sporangia are homosporous, thick walled and their development is eusporangiate. Spores were in tetrads. Stems cylindrical, vascular anatomy show lobed protostete and xylem was centrarch.

(*ii*) Trimerophytophyta : Plant body has monopodial branching in its main axis where as lateral axis has dichotomous or trifurcate branching. Surface of both axis were smooth, punctate or spiny. Branching differentiated into fertile and sterile axes. Fertile branches bear terminal sporangia which were aggregated at tips of dichotomous branches. Sporangia homosporous and development in eusporangiate. Stem solid, with protostele and centrarch xylem.

(*iii*) Zosterophyllophyta : Plant body rootless, leafless and branched dichotomously or pseudomonopodially, Protostelic stem with exarch xylem, xylem strands elliptic or terete with scalariform tracheids; Globose or reniform sporangia borne an lateral stem tips which were often aggregated into terminal clusters.

(*iv*) Psilotophyta : Plant body is differentiated into an underground rhizome and aerial shoot, underground rhizome covered with rhizoids, true root absent;aerial shoots bear minute scale like lateral appendages. Two to three lobed synangia associated with fertile appendges are found on aerial shoots; Plants homosporous. Multiciliate antherozoids present. Development of embryo is exoscopic and are without suspensor.

(*v*) Lycopodiophyta : Plant body well differentiated into root, stem and leaf, leaves microphyllous with single vein, Vascular tissue system is devoid of leaf gaps; Sporangia borne on adaxial surface of fertile leaf known as sporophyll, Plants homosporous as well as heterosporous, Antherozoids bi-to multiciliate, Development of embryo is endoscopic.

(*vi*) Sphenophyta : Plant body differentiated into leaf, stem and root, whorls of simple leaves are found on nodes of stems; Internodes of stem and branches longitudinally ridged; Leaf gaps absent in vascular arrangement of stems, Sporangia borne on sporangiophore; Number of sporangia on sporangiophore may vary from one to many, Antherozoids are multiciliate, Embryo development is exoscopic and embryo lacks a suspensor.

(*vii*) Pterophyta : Plant body differentiated into leaf stem and root (with few exceptions), Leaves are prominent and megaphyllous, Leaf gaps found in protostelic stem. Sporangia usually borne on margin or abaxial surface of fertile leaves; Antherozoids multiciliate and embryogeny may be either exoscopic or endoscopic.

QUESTIONS

ESSAY TYPE

1. Describe the characteristic features of pteridophytes. Give a brief account of the classification of pteridophytes also.
2. Write an essay on Alternation of generations in pteridophytes Or What do you understand by alternation of generations? Discuss with particular reference to pteridophytes.
3. What do you know of Antithetic and Transformation theories? Explain these with reference to alternation of generation.
4. Give an illustrated account of origin of vascular cryptogams.
5. Give a detailed account of various systems of classification of pteridophytes. Which system of classification is regarded as the best and why?
6. Discuss the classification of pteridophyta.
7. Give an account of classification of pteridophytes given by Sporne.
8. "Pteridophytes are said to form a bridge between Bryophytes and Gymnosperms". Explain giving reasons.
9. Give a diagrammatic representation of the geological Time scale, indicating therein the chief events and the appearance and disappearance of major plant groups.
10. With the help of suitable sketches write a short essay on Telome theory.
11. Describe the occurrence of Apogamy in Pteridophyta and discuss its significance.
12. Give an outline classification of Pteridophytes. Mention the main features of various classes and orders with examples. **(Kumaon 2004)**
13. Describe important features of Pteridophytes and Gymnosperms. How these groups are differentiated from each other?
14. Give the outline of classification of Takhtajan and Zimmerman (1966) and discuss the general characters of Pteridophytes. **(Kumaon, 2000)**
15. Give the classification of Pteridophytes based on Eames and Sporne's Classification.
16. Give an account of classification of Pteridophytes. Name the orders of the genera included in your course.
17. Give a detailed account of any system of classification of pteridophytes.
18. Write an essay on phylogeny and evolutionary tendencies in pteridophytes.
19. What is Telome theory? Discuss its importance in tracing the evolution in pteridophytes. **(Rohilkhand, M.Sc. 2000)**
20. "Pteridophytes were the simplest vascular plants." Discuss.
21. (*a*) What are fossils? How are they classified? Add a note on the importance of fossils. **(Kerala, 2000)**

    (*b*) What are fossils? Write various types of fossils studied by you. **(Nagpur, 2002)**
22. Describe the modern system of classification of pteridophytes upto the rank of orders.
23. Define Heterospory? Trace its origin in pteridophytes and point out its segnificance.
24. Pteridophyta is an intermediate between between Bryophyta and Spermatophyta. Elaborate the statement. Mention the origin and evolution of vascular structure in Pteridophyta. **(Guwahati, 2000)**
25. Write a brief essay on the origin of Alternation of generations.
26. Write a brief account of apospory, under the heads
    (*i*) Cytology and artificial induction,
    (*ii*) Causes of apospory and
    (*iii*) Significance of apospory.
27. Write an essay on the origin of vascular cryptogams.
28. Give a detailed account of the origin of alternation of generation.
29. What do you know of the origin of vascular cryptogams? Discuss in detail.
30. (*a*) Discuss in detail the evolution of the sporophyte in pteridophytes.

    (*b*) With the help of suitable diagrams, describe the evolution of stele in pteridophytes. **(Kumaon, 2004)**
31. What is the function of elaters?
32. What is columella?
33. What is heterospory?**(Kuvempu Univ., 2005)**
34. What do you understand by heterospory? **(Garhwal Univ., 2005)**
35. Explain the importance of study of fossils. **(Garhwal Univ., 2005)**
36. (*a*) Define obligate apogamy.
    (*b*) Define synangia, give example.
    (*c*) What is sori? **(M.S. Univ., Tirun., 2005)**
37. Elucidate the sporangial development in pteridophytes. **(M.S. Univ., Tirun., 2005)**

into a single order **Psilophytales** which is further spilt up into families.

(ii)* Class Psilotopsida :** It includes the order **Psilotales** which is represented by two living genera ***Psilotum and Tmesipteris.

Class : PSILOPHYTOPSIDA

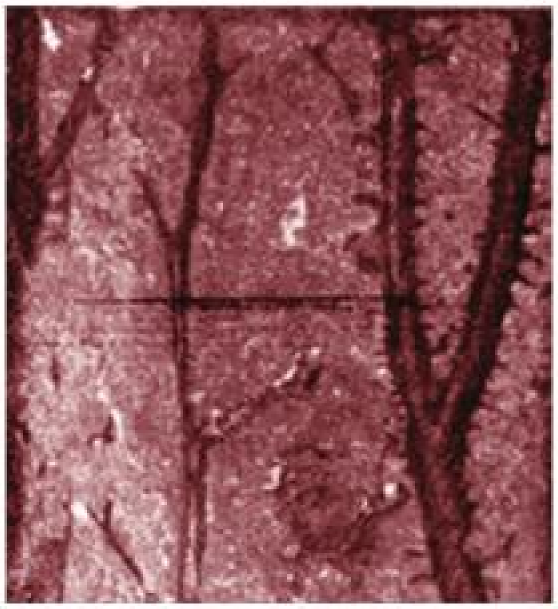
Characteristic features :

1. *All the plants are extinct.*
2. *Only sporophyte are known so far.*
3. *Plant body is distinguished into rhizomes and aerial branches which are more or less dichotomously branched.*
4. *Roots are completely lacking, but at places unicellular rhizoids are present in tufts.*
5. *Aerial branches are naked or has spirally arranged small appendages.*
6. *Thick walled homosporous sporangia are present and their position is terminal or lateral.*
7. *Stele is simple protostele.*

Order Psilophytales

They are the simplest extinct vascular plants that were discovered among the rocks of the Early Devonian period of the Palaeozoic age. Among these plants, the first to be recorded in 1858 was Sir William Dawson's ***Psilophyton princeps*** that was discovered from the Gaspe Sandstone. Later it was also recorded in beds of various Devonian horizons in many countries, such as the United States, Scotland, Norway and Belgium. It is the first plant with which our knowledge of the group **Psilophytales** started.

The group Psilophytales was actually recognised and named when the Rhynie discoveries came into light. Our present accurate 'knowledge of these simple vascular plants is mostly due to investigations of the Rhynie chert-bed. This locality is in Aberdeenshire, and the bed was discovered by the geologist Dr. Mackie in 1913. The plants have been thoroughly worked out by Dr. Kidston and Prof. Lang, whose results are recorded in their remarkable series of memoirs that were published in 1917 to 1921.



***Psilophyton princeps*, first extinct vascular plant to be recorded in 1858**

The Psilophytales are most prevalent in the lower and the middle Devonian period. They have been recorded by some in the upper Devonian rocks but the discoveries are not entirely free from doubt. They are characterised by : — 1. A simple plant body distinguished into a rhizome and an aerial region. 2. Absence of roots. 3. Rhizoids arise in tufts from rhizome. 4. The stems branch dichotomously and are naked or covered with small spinous outgrowth or reduced leaves. 5. Vasculature is a protostele. 6. Sporangia are terminal and may occur solitary or in groups or in simple recemes. They are not associated with any kind of sporophylls. They have a single spore cavity. 7. The wall of the sporangium is several cell layers thick. 8. They are homosporous, spores arranged in tetrads. These characteristics are shared by majority of Psilophytales, but variations are there. In ***Asteroxylon*** the sporangia are now reported to occur singly a little above the leaf (cauline). For this reason it has been included by some authors under the Lycophyta (Bierhorst, 1971).

CLASSIFICATION

Krausel and Hirmer have put forth a scheme of classification of the group. They divide it into 9 families including more than 20 genera. Out of these 9 families five are most firmly established.

organisation. The centre is occupied by xylem tracheids (Fig. 2.2) that showed traces of annular and sometimes of spiral thickenings. It has also been observed in certain cases that the tracheids in the centre are smaller than the tracheids surrounding them. It reflected on the endarch differentiation of the xylem tissue. The cells surrounding the xylem tissues were thin-walled and without any intercellular spaces. In longitudinal sections these cells appear to be elongated with oblique end walls. This tissue appears to be stelar in nature and is most probably phloem. There are no traces of sieve plates or pores in the cells of phloem and it is in this respect that this tissue differs from the phloem of the living Pteridophytes. Satterthwait and Schopf (1972) reported the occurrence of numerous pores (3-8 µ in diam.) distributed along the lateral cell walls in this zone of tissue. In face view these pores appear to be composed of circular sub-units. They reported the presence of sieve tubes and parenchyma cells in the phloem zone and also observed the presence of pit fields in the lateral cell walls and inclined end walls of sieve tubes. The pericycle and endodermal layers were lacking.

In the rhizome there is no distinction between the outer and inner cortex and the xylem strands consist of but fewer tracheids.

The growing point consists of numerous dividing cells. There is no apical cell.

Sporangia

They are club-shaped or cylindrical structures (Fig 2.1) borne terminally on the fine aerial branches (4 m.m. long and 1.4 m.m. broad). Their wall is three layered : an outer epidermal layer, a middle three cell rows thick layer and an inner layer. The outer layer is heavily cutinised. The sporangium contained large number of spores arranged in tetrads like the modern ferns. They are homosporous and measured 40 µ in diameter. The spore wall must have been tough so as to preserve them so nicely. The spores were trilete. The development of the sporangium was of **eusporangiate type** as it developed from a group or a row of superficial cells that divided periclinally to form an outer primary wall layer and an inner layer of primary sporogenous cells.

RHYNIA MAJOR

It is wholly a leafless plant (Fig. 2.3) distinctly differentiated into a rhizomatous portion bearing tufts of rhizoids and an aerial portion quite naked and devoid of any hemispherical outgrowths as are found in the other species. Branching is by forking dichotomy. No adventitious branches are present. The estimated height is about 20 cm. or even more and diameter 6 mm. The sporangia borne at the ends of the branches (Fig. 2.3, B) are about 12 m.m. long and 4 m.m. in breadth. The spores were about 65 µ in diameter.

Internal structure too is very simple and agrees in all respects to that of ***Rhynia gwynne-vaughani.*** Stele is a typical protostele. Its larger size, absence of hemispherical outgrowths and the absence of adventitious branches are the points that differentiate this species from the smaller ***Rhynia gwynne-vaughani***.

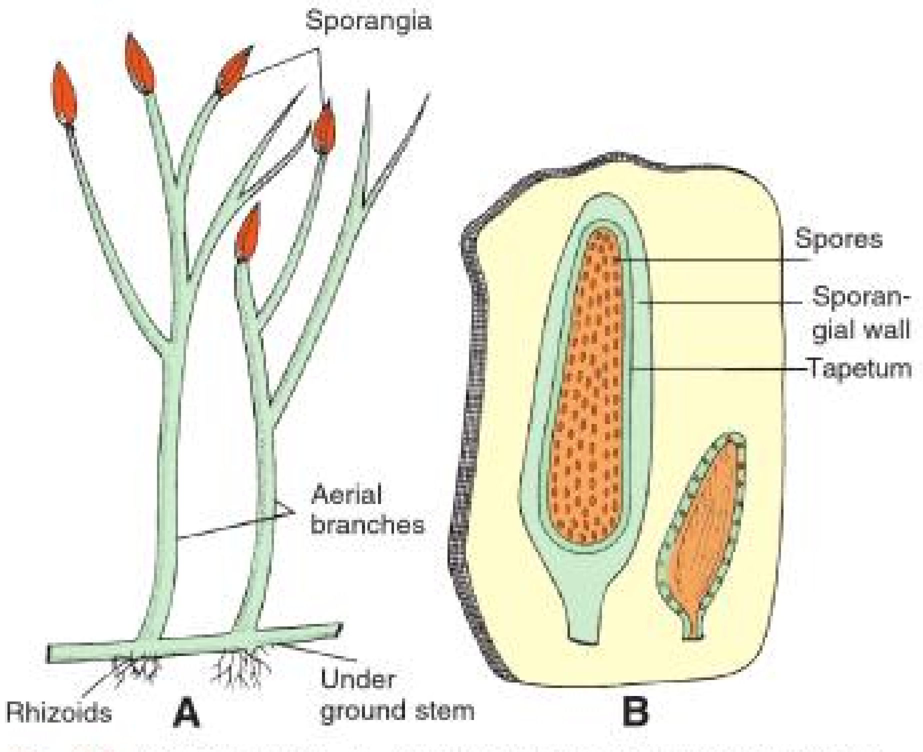


Fig. 2.3. ***Rhynia major***. **A.** Reconstruction of a complete plant; **B.** sporangia. (After Kidston and Lang).

DISCUSSION

In the words of Dr. D.H. Scott, "the ***Rhyniaceae***, simple as they are, show such a remarkable combination of characters and they have been placed by different botanists in three of the great sub-kingdoms of plants. Kidston and Lang, whom I have followed, assign them to the Pteridophytes, because the spore bearing generation was a vascular plant; my late friend Dr. Newell Arber, in whose time only ***Rhynia*** had been described referred the genus to Thallophytes, on the ground of its undifferentiated thalloid stem : the family has also been included under Bryophytes, on account of the characters presented by ***Horneophyton*** and ***Sporogonites.*** This is a very extraordinary position and shows that Rhyniaceae are a unique race of plants."

Rhyniaceae can very well be treated as a synthetic group of plants combining the characters of vascular cryptogams and the bryophytes on one hand and retaining some of the characters of the thallophytes on the other side. Such a conclusion is justified by the structural facts actually known to us. The question arises whether the Rhyniaceae were really primitive plants. Their environments were quite unfavourable and it is just possible that the plants became reduced due to environmental stresses.

According to Leclercq (1954) Devonian Rhynie flora can not be considered to be the representative of earliest land plants. This is particularly true for **Rhynia** as **Asteroxylon** (more complex form) co-existed with it. Fossil records of Silurian vascular plants (**Yarravia, Hedia corymbosa, Cooksonia** and **Zosterophyllum** ***sp***.) also confirms this view. These findings of fossil records make it doubtful wheather to consider **Rhynia** as most primitive land vascular plant or not. Whatever the case may be the facts remain that Rhyniaceae are a group of simplest and the ancient of the plants known to us. The character which make **Rhynia** a simple and primitive plant are :

1. Plant body is not differentiated into stem and roots.
2. Presence of uniform dichotomous branching in whole plant.
3. Leaves are absent and appendages (hemispherical outgrowth) can not be considered leaf.
4. Stele very simple with a slender strand of tracheids.
5. Sporangia were the modified branch tips.

Out of the living Pteridophytes the ***Rhyniaceae*** bear resemblances with the Psilotales. The order includes two living representatives, ***i.e***., ***Psilotum*** and ***Tmesipteris***. The aerial stems of ***Psilotum*** are devoid of true leaves like ***Rhynia*** and are in the same fashion, dichotomously branched. There aare no roots. The underground rhizomes are provided with tufts of unseptate rhizoids. ***Tmesipteris*** does bear leaf-like appendages but they are flattened laterally and merge with the stem by strong decurrent bases. The sporangia are borne on short branches that arise laterally from the stem.

The bullbous rhizome of ***Horneophyton*** recalls the protocorm of some members of the Lycopodiales, e.g., ***Phylloglossum.*** Protocorms always develop before the roots and are connected to the soil by means of rhizoids.

The lowly organised body of the ***Rhyniaceae*** attaches it with algae. It is only the appearance of vascular system that separates them from the Thallophytes. Algae having as complex a plant body as that of ***Rhynia*** do exist. They have a well developed rhizome and upright dichotomously branched aerial parts bearing tetrasporangia. The more commonly accepted opinion is the early pteridophytes(Psilophytales) had an algal ancestor rather than a bryophyte.

The fructifications of ***Rhyniaceae*** suggest a close relationship with the Bryophytes. The overarching sporogenous layer in ***Horneophyton*** and ***Sporogonites*** and the presence of columella are suggestive of affinities with the Bryophytes. The sporangia are terminal. We cannot extend our comparisons to the gametophytes as the prothalli of Psilophytales have not been discovered. ***Rhyniaceae*** lack annulus and no definite mechanism of dehiscence has been found out.

Krausel (1957) discovered from the upper carboniferous of the Ruhr region a psilophyte of doubtful position. He named it as ***Paulophyton jongmansi*** (Fig. 2.9). It has a 3 cm. broad axis bearing equally and unequally dichotomising branches. The ultimate branches are equal in length and terminate in a swollen tip presumed to have been a sporangium.

Trimerophyton robustius, (Fig. 2.8, B) is another member related to ***Psilophyton*** and is represented by a short axis that is nearly 1 cm. in thickness. It bears lateral branches that branch in a trichotomous manner and then dichotomously and ultimately bear terminal sporangia. ***Taeniocrada dechniana*** (Fig. 2.8A) discovered in lower Devonian of Rhineland possessed ribbon-shaped and dichotomously branched axis bearing terminal sporangia. ***T. langi*** was discovered from the lower Devonian of Belgium. In this species shoots bear stalked sporangia (Fig. 2.8, F,G) that arise laterally and are ovoid in shape. Its identity is doubtful because spores have not been found in the sporangia.

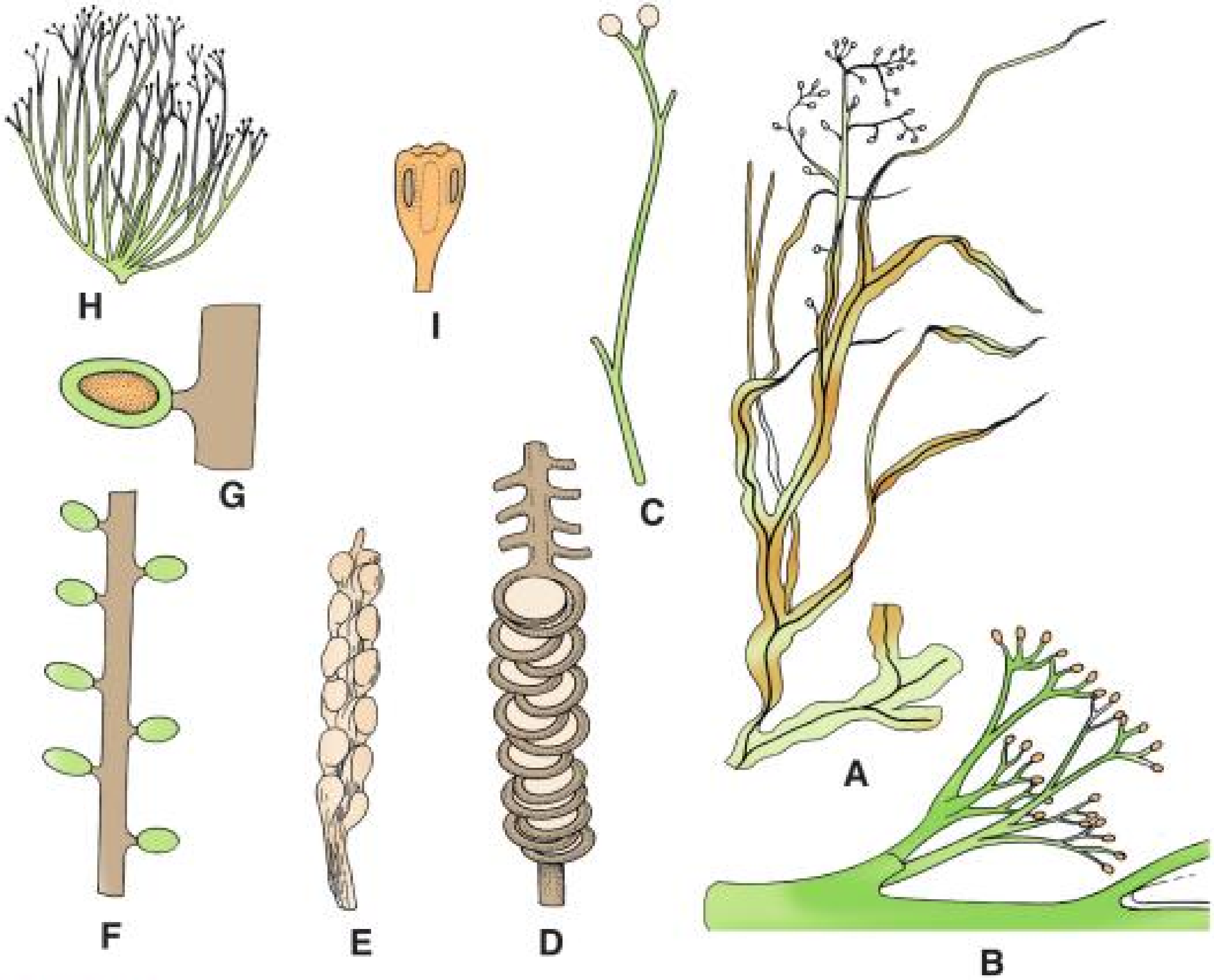


Fig. 2.8 (A–I). **A.** ***Taeniocrada decheniana***; **B.** ***Trimerophyton robustius***; **C.** ***Cooksonia*** sp; **D.** ***Pectinophyton bipectinatum***; **E.** ***Bucheria ovata***; **H. Hicklingia** (after Banks, 1968 a); **I.** ***Yarravia***– a Sporangium (after Andrews, 1959); **F, G.** ***Taenocrada langi*** (from Andrews)

The family **Pseudosporochnaceae**

It is characterised by the genus ***Pseudosporochnus*** (Fig. 2. 10). It was reported from the Bohemian Middle Devonian period. It has also been reported from Norway and Scotland but the fossils from Bohemia are nicely preserved and have been properly investigated.

Banks' perception about evolutionary specialization came after the transfer of ***Asteroxylon*** to Lycopsida was confirmed.

Niklas (1979) reaffirms the above line of evolution in Psilophytales following studies on fossil records and its chemical constituents like sterols, fatty acids, lignin and aromatic acids.

QUESTIONS

ESSAY TYPE

1. Describe the salient features of Psilophytales and describe its phylogenetic significance.
2. Give an account of Psilophytales and discuss how they have cleaned our notions on the phylogeny of vascular plants.
3. Psilophytes were the simplest vascular plants. Discuss.
4. Write a short essay on evolutionary significance of Psilophytes.
5. Describe the morphological and anatomical structure of an adult sporophyte of ***Rhynia***. **(Awadh 2000)**
6. What is the age and locality of ***Rhynia***? Mention the name of its species and their salient features. **(Allahabad, 2003)**
7. Describe a Devonian vascular plant.
8. How many species of ***Rhynia*** are known? Write their names with the help of suitable sketches, describe their salient features and also mention the systematic position of the genus. **(Lucknow, 2001; Allahabad, 2002)**
9. Mention the age and locality of ***Rhynia*** and point out the similarities and differences between ***R. major*** and ***R. gwynne vaughanii***.
10. Give an illustrated account of the morphological structure of ***Rhynia***.
11. Describe the morphology and anatomy of ***Rhynia***. How can you consider it as the most primitive vascular land plant.
12. Describe the morphological and phylogenetic importance of ***Rhynia***.
13. Draw labelled diagrams of the T. S. of aerial stem and L. S. of the sporangium of ***Rhynia***. What characters of land plants does it show? **(Poorvanchal, 2000)**
14. Describe the structure of sporophyte of ***Rhynia***. How can you consider it as the most primitive land plant?
15. Describe the structure of the earliest known vascular plants and comment briefly upon their fructifications.
16. Write what you know about ***Rhynia***.
17. Write the following about ***Rhynia***
    (*a*) Classification
    (*b*) T. S. aerial stem
    (*c*) L. S. Sporangium
18. Mention the characteristic features of Psilophytales. Write a short account of early vascular plants studied by you.
19. Are Psilophytales starting or resulting points? Discuss. **(Awadh, M.Sc, 2000)**
20. Describe in detail the external morphology of ***Rhynia*** plant and anatomy of its reproductive part with the views on its gametophyte.
21. Describe briefly the morphology and anatomy of the vegetative and reproductive parts of ***Rhynia***.
22. Comment on the common features of Psilophytales and Psilotales. **(Calicut, 2001)**
23. With suitable illustrations, give an account of ***Rhynia***. How does it differ from ***Psilotum*** ?
24. Discuss the evolutionary importance of ***Rhynia***. Place it in its systematic position.
25. Describe the distribution and structure (both external and internal) of aerial branch of ***Rhynia***.
26. Describe the life history of ***Rhynia***.
27. Give a detailed account of the morphology and anatomy of ***Asteroxylon***.
28. Describe ***Psilophyton*** and ***Pseudosporochnus***, with labelled diagrams.

    or

    Describe a Devonian Vascular plant. Illustrate your answer with suitable diagrams. **(Lucknow, 2005)**
29. Discuss the various genera of ***Psilophytales***. Give a diagrammatic account of ***Rhynia*** and ***Asteroxylon***.
30. "***Zosterophyllum*** occupies a special position". Discuss the statement.
31. How many genera have been placed in the class Psilophytopsida? With illustrated diagrams, describe two genera in detail.
32. Write an account of ***Rhynia***. **(Mysore Univ. 2004)**

Psilotum nudum

CHAPTER 3

Division– Psilophyta Class– Psilotopsida

- Introduction
- Distinguishing features
- Description of ***Psilotum***/Swartz
- Description of ***Tmesipteris***/Berhardi
- Difference between ***Psilotum*** and ***Tmesipteris***
- Affinities of Psilotales
- Significance and Phylogeny of Psilophyta

Introduction

The order Psilotales is closely related to the extinct order Psilophytales and comprises two genera. These are ***Psilotum*** (2 species) and ***Tmesipteris*** (10 species). Both these genera are placed in family ***Psilotaceae***. It has now been proposed to refer ***Tmesipteris*** to a separate family ***Tmesipteridaceae.*** Bierhorst (1971) has raised the status of ***Psilotaceae*** and has placed it in the class ***Filicopsida*** somewhere near the family ***Stromatopteridaceae.*** Lovis (1977) accepted Bierhorst's contention in considering the

3. The inner cortex is composed of several layers of cells which show gradual reduction of the thickness of cell walls as we proceed towards the stelar region. The cells contain starch grains. This region is also called the storage region.

The cortex becomes entirely chlorenchymatous in the younger portions of the aerial axes.

The endodermal cells have distinct casparian strips. The pericycle is single layered and consists of thin-walled cells.

Vascular Region

The vascular region is surrounded by a single layer of pericycle and an endodermis. It consists of xylem and phloem; the latter completely surrounds the former. The following variations in the vasculature of rhizome and at various levels of a aerial branches were observed by Bower (1935) and Pilot (1950) :

(*i*) In the rhizome it is a protostele with central core of xylem completely surrounded by phloem. The xylem core is not starshaped or lobed (Fig. 3.4). There is no pith.

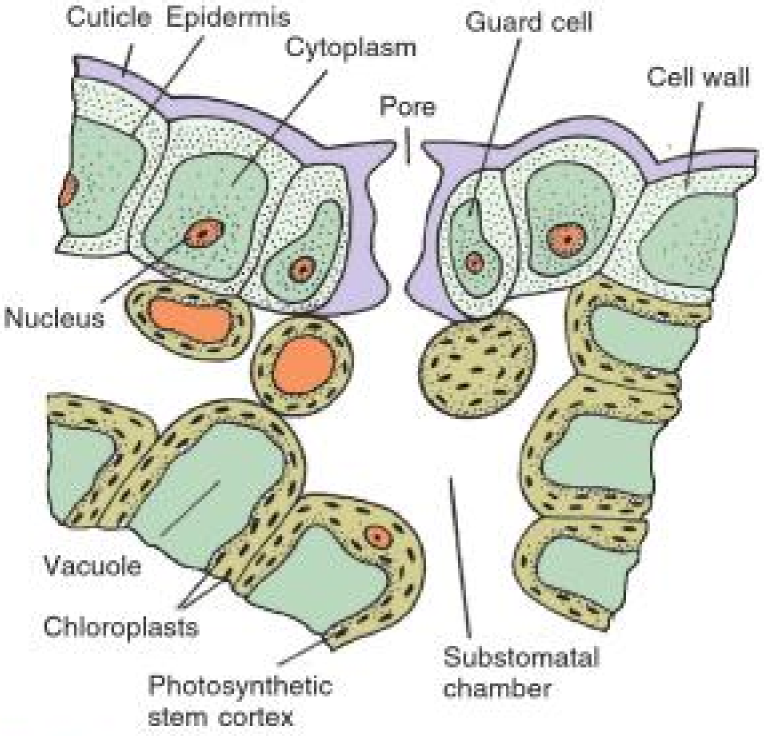


Fig. 3.3. ***Psilotum nudum.*** T.S. portion of stem showing epidermis and stoma.

(*ii*) In the transit zone between rhizome and aerial shoot the xylem becomes lobed and as many as 10 lobes can be counted. There is no pith. The protoxylem occupies the tips of the lobes. The phloem occurs in between the lobes and forms irregular patches. Here the stele is actinostelic protostele.

(*iii*) In the middle of aerial shoot the number of xylem lobes is reduced to 5 or 7 and pith appears in the centre (Fig. 3.2, A). Here it changes from protostele to a siphonostele.

(*iv*) In the apical regions of the aerial shoot the outline of the stele is triangular and the xylem splits into two distinct patches (Fig. 3.2, B).

In all these cases the xylem is **exarch**. It consists of only tracheids. The protoxylem has spiral tracheids whereas the metaxylem tracheids are scalariform or pitted. The phloem consists of sieve tubes and phloem parenchyma. The sieve tubes are vertically elongated with slight lignification at the angles and have sieve plates in both lateral and terminal walls. They lack nuclei at maturity, but some spherical bodies have been reported in the cells (Ford, 1904; Stiles, 1910, Essau, 1953).

In the region of the rhizome a transverse section reveals a well defined epidermis (Fig. 3.4, A), followed by a broad zone of cortex. The cortex has an outer mycorrhizic zone (Fig. 3.4, A), middle zone of starch storing cells and an inner cortex whose cells contain phlobaphene or tannin anhydrides. There is a distinct endodermis surrounding a single layered pericycle which in turn encircles the protostele (Fig. 3.4, A). The protostele has a central core of exarch xylem surrounded completely by phloem.

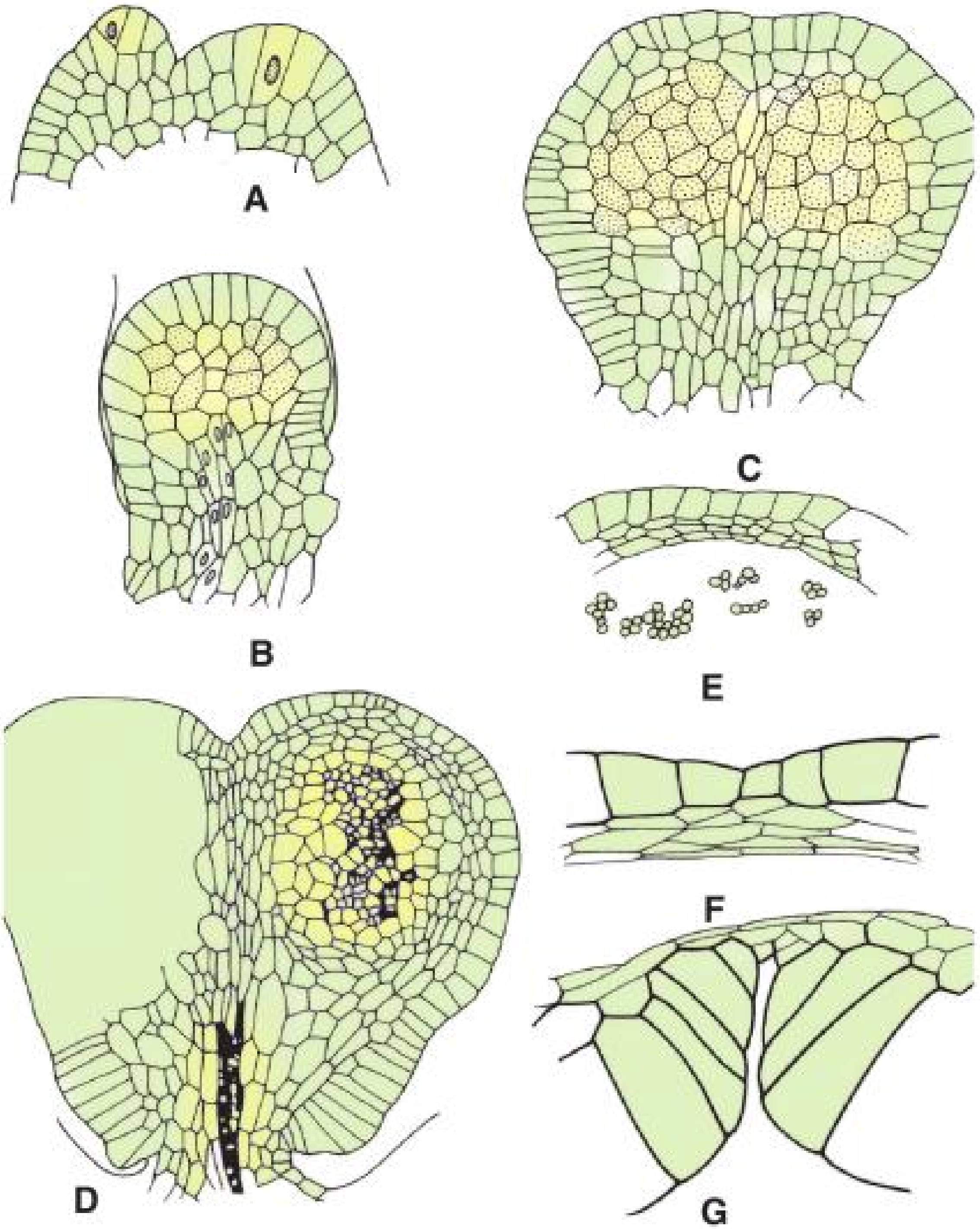


Fig. 3.6a (A–D). ***Psilotum nudum.*** **A.** L.S. Aerial shoot apex showing a fertile appendage towards its left; **B–D.** Stages in the development of Synangium ; **E.** T.S. Through the wall of sporangium; **G.** Shows line of dehiscence. (After Bierhorst).

(1956) opposes this view and believes that the sporangium arises earlier than the bilobed appendage which arises later as a lateral outgrowth from the sporangial stalk. Bierhorst describes the development as follows :

Each lateral outgrowth destined to develop into a trilobed sporangium, grows by means of an apical cell to form a short multicellular fertile axis (stalk of sporangium). Three separate surface initials make their appearance at the summit of the fertile axis and indicate the sites of three sporangial locules (chambers). Each initial divides periclinally to form an outer primary wall initial and an inner primary sporogenous cell (Fig. 3.6, B). The former undergoes periclinal and anticlinal divisions to form a 3 to 4 layered thick wall (Fig. 3.6, D). The primary sporogenous cell divides to form a mass of sporogenous cells, some of which later on develop into spore mother cells. The development of sporangium is, therefore, eusporangiate.

vascular strand in the prothallus is an unusual character. Holloway (1939) studied the growth of prothallus in ***P. nudum*** and described the occurrence of interrupted vascular system that was essentially a protostele. He found that the protostele was periodically interrupted by intervening regions of parenchyma. Holloway found that growth in these prothalli was intermittent. An active period of apical growth accompanied by the differentiation of vascular tissue was followed by an inactive period of growth when there was no vascularisation. Again a period of active growth followed by differentiation of vascular tissue was there. This resulted in an interrupted vasculature. Bierhorst (1953) atributes this discontinuity to be due to the injury of the apical cell or region by the soil particles through which it grows. The vascular strand originates within the apical region (Fig. 3.8$_a$A).

Sexual Reproduction

The gametophytes are monoecious and sex organs are scattered over the surface of the gametophyte (Fig. 3.9) and occur intermingled. They start appearing along the sides of apical portion of the prothallus.

Antheridium

The superficial antheridial initial divides by a periclinal wall into an outer **jacket initial** and an **inner primary spermatogenous** cell or **primary androgonial cell** (Fig. 3.10, B). The jacket initial divides by repeated anticlinal walls to form a single layered wall of antheridium (Fig. 3.10, C). The primary spermatogenous cell divides by an anticlinal wall to form two cells (Fig. 3.10, C). Later divisions take place in various planes to produce a mass of spermatogenous cells (Fig. 3.10, D, E). At a stage when the spermatogenous tissue is composed of 8 cells, the antheridium bulges above the surface as a minute outgrowth. Further divisions within the antheridium and differential cell enlargement of the tissue below the antheridium lead to the projection of the entire sex organ above the surface (Fig. 3.9, B). The spermatogenous tissue, surrounded by a single layered wall gives rise to **sperm mother** cells or the **spermatocytes** (Fig. 3.10, F). The spermatocytes later metamorphose into spirally coiled and multi-flagellate **spermatozoids** (Fig. 3.10, H). When mature the antheridial wall dehisces by the breaking of one of its cells along the sides (Bierhorst, 1954). The spermatozoids come out through this pore. The number of spermatozoids per antheridium varies from 32, 64, 128 to 512. In some abnormal antheridia (Holloway 1939, Bierhorst 1954) the cells of antheridial wall divide repeatedly and grow inwards and crush some of the spermatocytes. This results in lessening of the number of spermatozoids. The ratio of presence of such abnormal antheridia is one in ten.

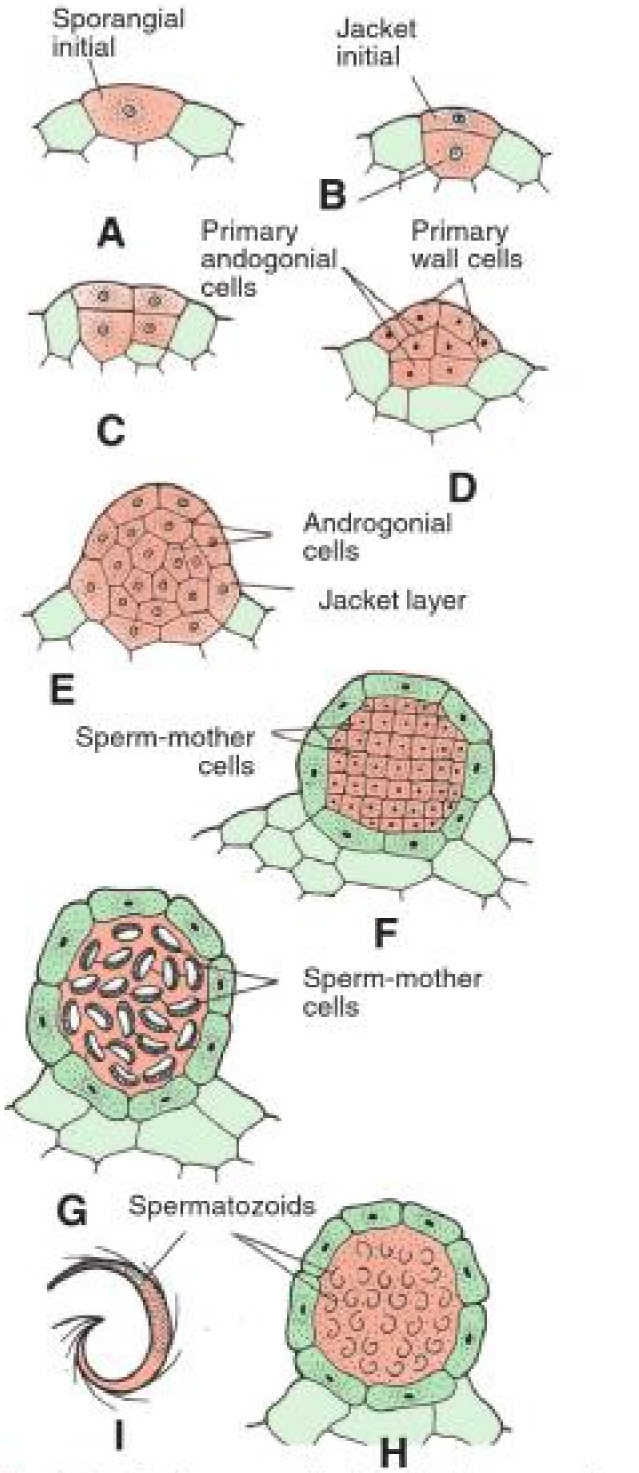


Fig. 3.10. Various stages in the development of antheridium in *Psilotum nudum*. (After Lawson)

The antheridia which develop on the older portions of the prothallus are smaller in size and produce only thirty two spermatozoids.

A mature antheridium (Fig. 3, 10, G, H) is more or less a globular structure without any stalk. It consists of a single layered wall with enclosed spermatocytes.

Archegonium

It develops from a single superficial cell (Fig. 3.11, A) which divides periclinally into an outer **cover cell** and an inner **central cell.** The cover cell **divides** by two intersecting anticlinal walls to form four cells, which act as initials of the four **rows** of the archegonial neck (Fig. 3.11, C). These four cells divide by repeated transverse walls to form four longitudinal rows of the neck, each row from 4—6 cells high. The **central cell** divides (when the neck is only three cells long) by a transverse wall into an upper **primary canal cell** and a lower **primary ventral cell** (Fig. 3.11, D). The former divides by a transverse wall to form two neck canal cells. In most cases the wall separating the two neck canal nuclei has not been observed (Fig. 3.11, E). The **primary ventral cell** divides transversely (Fig. 3.11, F) into an upper **ventral canal cell** and a ***lower* egg cell.** Bierhorst (1954) has reported a case where the central cell functions directly as the egg cell.

The necks of the archegonia are straight, and the venter is embedded in the tissue of the gametophyte.

A mature archegonium consists of 4 longitudinal rows of neck cells, each row 4 to 6 cells high. The neck encloses a neck canal (Fig. 3.11, F) with two **neck canal nuclei** or two **neck canal cells.** There is a single **ventral canal cell** and a single **egg cell.** There is no sterile wall surrounding the venter as this portion is embedded in the tissue of the gametophyte.

As the archegonium matures the cell walls between upper tiers of neck cells become cutinised and the upper part of the neck breaks away (Fig. 3.11, G).

Bierhorst (1954) states that this breaking off of the neck takes place after the process of fertilisation. Earlier workers believed it to have taken place before the act of fertilisation.

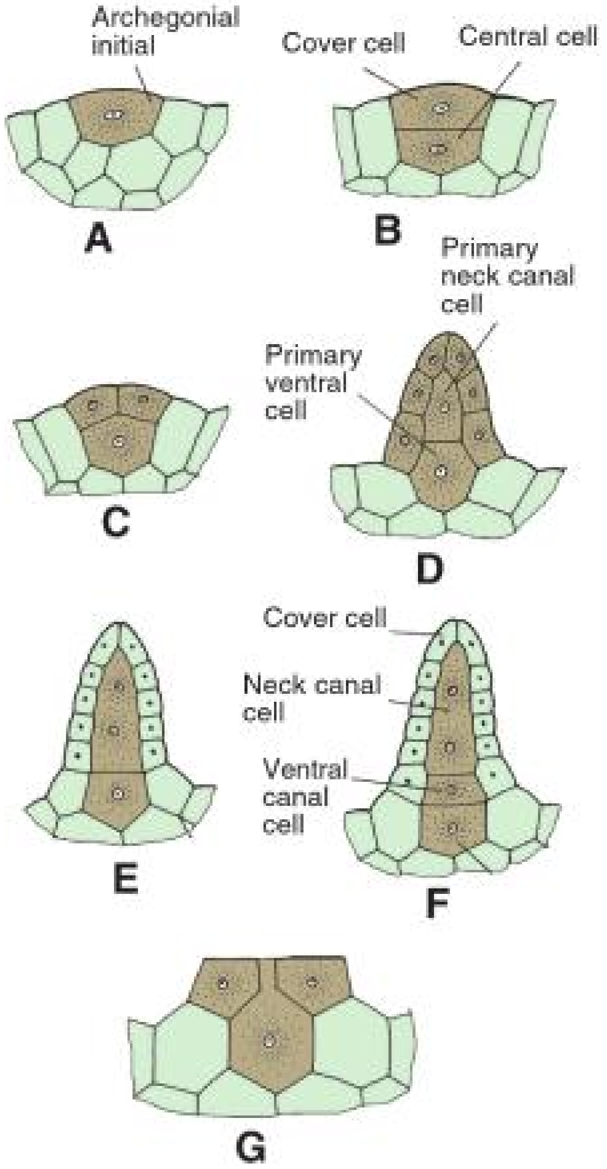


Fig. 3.11. Stages in the development of Archegonium in *Psilotum nudum.* (After Bierhorst)

Prior to fertilisation, it appears, the usual disintegration of axial row of cells (neck canal cell and ventral canal cell) takes place. They absorb moisture, become mucilaginous and force open the uppermost tier of neck cells thus permitting the spermatozoids to enter the archegonial neck and reach the egg.

Fertilisation consists in the union of spermatozoid and the egg, followed by the fusion of the male and female nuclei (syngamy). There is every possibility that fertilisation many not even take place in the diploid or the polyploid gametophytes.

Vegetative Propagation of the Gametophyte

Holloway (1939) and Bierhorst (1953) reported the development of gemmae on the surface of the prothallus (Fig. 3.9, C, D). They appear at the tips of short, erect and multicellular outgrowths.

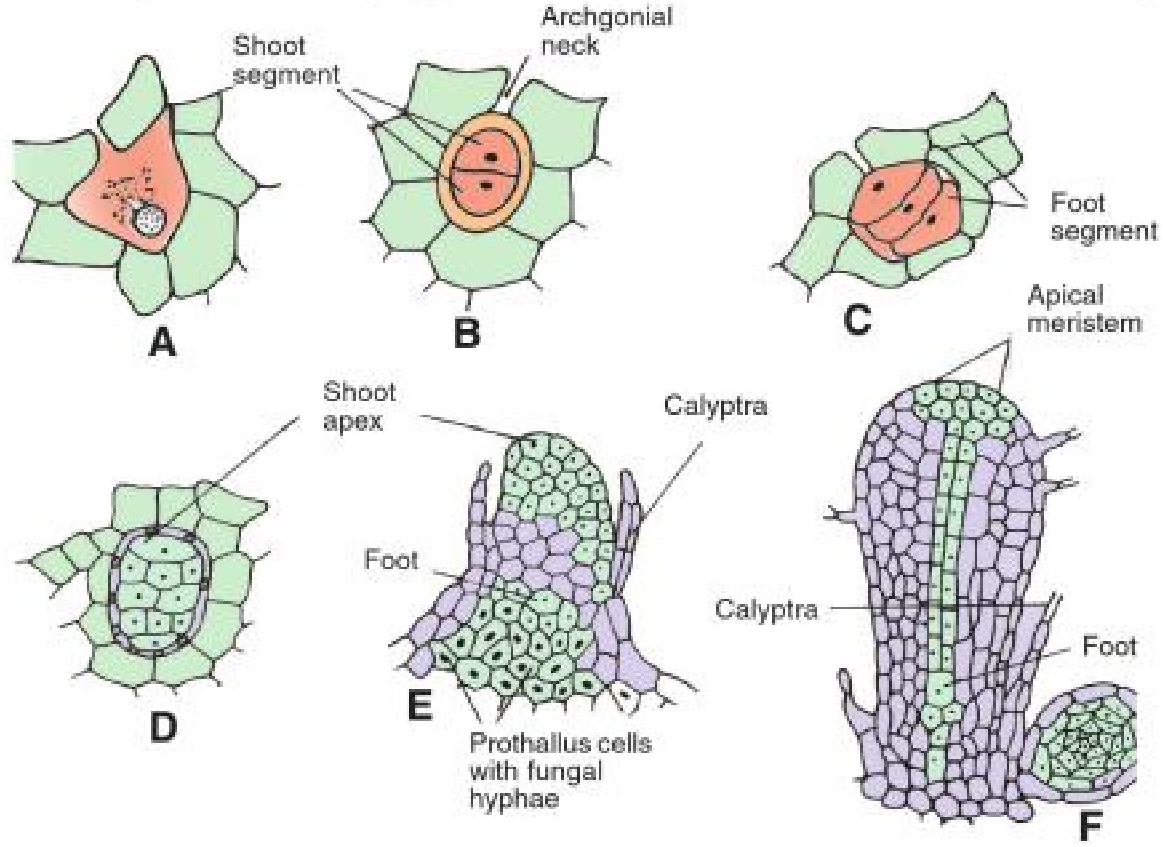


Fig. 3.12. ***Psilotum nudum.*** Various stages in the development of embryo (**A–E** after Bierhorst ; **F** after Holloway).

The terminal cell of this rhizoidlike outgrowth divides repeatedly to form an ovoid gemma-like structure that may contain 8 to 12 cells at maturity. These gemmae germinate to give rise to new prothalli. In addition to gemmae Holloway (1939) reported the formation of small outgrowths which develop from one or two surface cells that divide to form bud-like outgrowths. He named them as **vegetative buds.** They differ from gemma in their mode of origin. They do not arise on the tips of short outgrowths but directly on the prothallus.

The Embryo

The archegonial venter increases in size and the open neck is closed by the formation of calyptra (Fig. 3.12_a A,B). The fertilized egg or the zygote nucleus increases in size and moves to the inner end of the cell (Fig. 3.12_a B). In some cases it has been observed (Holloway, 1917 ; Bierhorst 1954) that the zygote nucleus protrudes into the archegonial neck and sometimes the protrusion is so pronounced that the nucleus appears to be an "attenuated beak." The nucleus is surrounded by a delicate membrane. The zygote divides first by a transverse wall into an **epibasal cell** or **shoot cell** (Fig. 3.12, B and Fig. 3.12_a C) towards the neck of the archegonium and a **hypobasal cell** or **foot segment** below. These cells are distinct by their larger nuclei. The nuclei contain distinct nucleoli.

The epibasal cell gives rise to the shoot system (both rhizome and the aerial branches) and the hypobasal cell divides in various planes to give rise to a bulbous foot. The epibasal and the hypobasal cells, each divide by a longitudinal or an oblique wall to give rise to a four celled stage (Fig. 3.12_a D). In Fig. 3.12_a D only the lower cell has divided. After this four celled stage the further divisions are somewhat irregular. The hypobasal cells divide by ten longitudinal divisions which divide the foot into a number of cells that are longer (Fig. 3.12_a E) than broad. Later some of the foot cells divide in

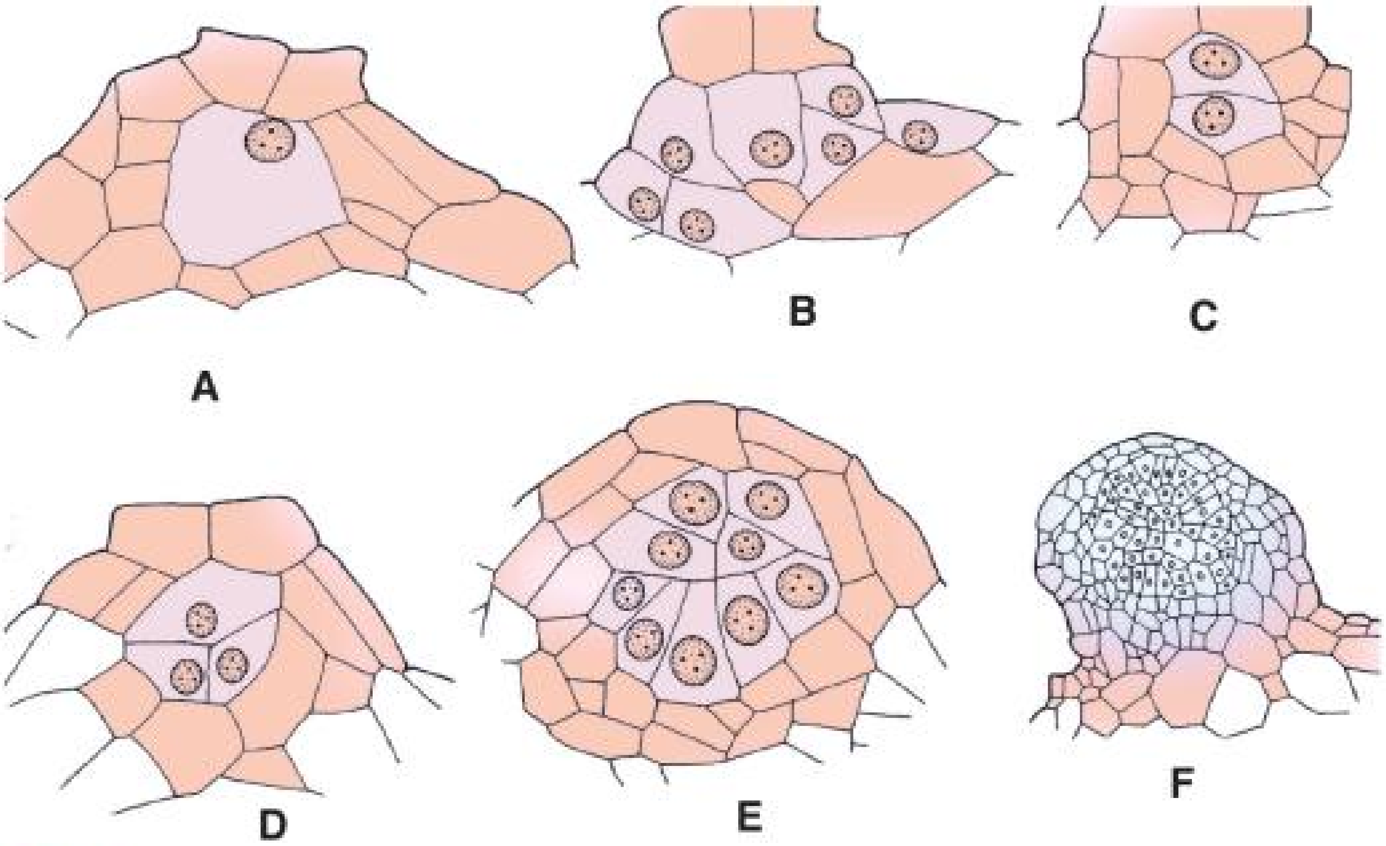


Fig. 3.12a ***Psilotum nudum*** **(A-F).** Stages in the development of embryo. **A–B.** Showing zygote enclosed within the calyptra; **C.** First transverse division of zygote into upper or epibasal (towards archegonial neck) shoot segment and lower or hypobasal foot segment; **D-E** Later stages of development; **F.** Showing well developed foot and shoot segment. (After Bierhorst)

a transverse plane and form finger like rows of cells which grow into the tissue of the gametophyte below and crush its cells. Rest of the foot cells undergo longitudinal divisions which increase the number of potential haustorium like processes (Fig.3.12_a, F and Fig. 3.12_b, B). The foot becomes bulbous and secures the sporophyte to the gametophyte and absorbs nutrition from it till the sporophyte becomes independent. While the foot is developing the epibasal cell divides in three different planes. (Fig. 3.12, C, D and 3. 12_a E). The first division of the epibasal cell or the rhizome initial, as mentioned earlier, is oblique to the first division of the zygote. The second division is nearly perpendicular to the first. Two subsequent divisions lead to the formation of a three sided apical cell of the young sporophyte (Fig. 3.12 D). At this stage the embryo bulges out as a prominent outgrowth on the surface of the gametophyte (Fig. 3.12, E). As a result of the activity of this apical cell the shoot soon grows vertically and becomes prominent (Fig. 3.12_b B). The surrounding cells of the gametophyte divide to form a calyptra-like outgrowth enveloping the young embryo. By further growth the embryo pierces through the calyptra (Fig, 3. 12 E,F). The young shoot soon establishes itself as a young axis with vascular tissue. It is the future rhizome which is at first unbranched, but undergoes branching at a later stage. The young rhizome detaches itself from the foot by the foot by the formation of a separation layer at the original boundary between the foot and shoot.

The rhizome continues to grow in length and branches repeatedly in a dichotomous manner. The tips of the ultimate branches turn upwards and develop into aerial branches that come out of the humus and grow erect.

The embryo of ***Psilotum*** is remarkably different from most of the other pteridophytes in lacking initials of suspensor, leaf and root. Apogamy has been reported in ***P. nudum*** (Bierhorst, 1971).

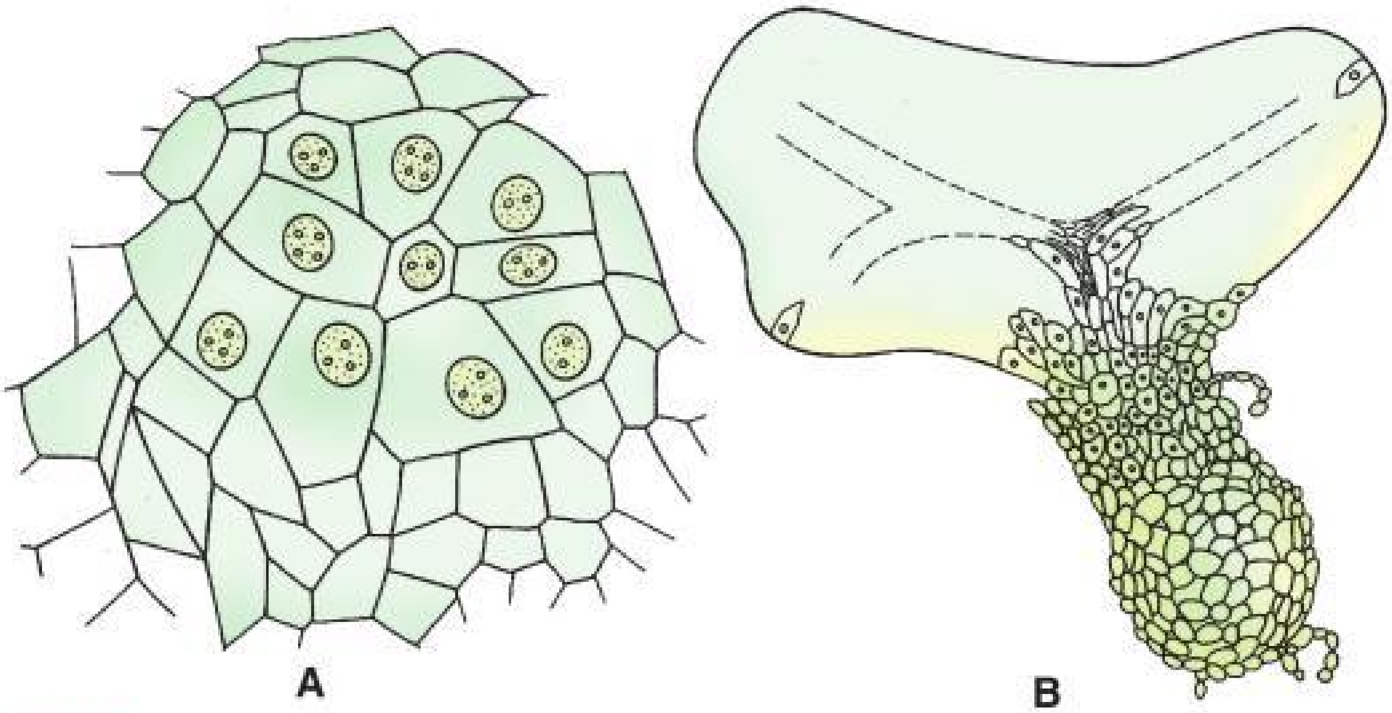


Fig. 3.12b. *Psilotum nudum* (A–B). **A.** Earlier stage in embryo development showing divisions in the shoot and foot segment; **B.** The embryo has pierced through the calyptra and shows the development of the vascular tissue. Also note the massive foot. (After Bierhorst, 1954)

TMESIPTERIS / BERNHARDI

T. lanceolata

Tmesipteris with about 10 species (Bierhorst, 1971) is a genus quite restricted in distribution. It is confined, to some islands in the South Pacific ocean, Australia, New Zealand, Tasmania, Polenesian islands and New Caledonia, Polenesian islands and New Caledonia. Majority of the species are epiphytes growing on tree trunks, aerial trunked stems of some tree ferns or in the humus formed by organic debris on the trees. It has also been collected from the root mantle of palms. ***T. tannensis*** (Fig 3.13 A) usually grows as pendulous epiphyte hanging freely from tree trunks. It has also been recorded growing on heaps of humus. ***T. vieillardi*** is a terrestrial species that has been found growing erect on ground in New Caledonia (Sahni, 1925 and Dangeard, 1926). The two other species that are commonly found include ***T. lanceolata*** and ***T. forsteri.***

Plant Body

T. tannensis

The plant body consists of a creeping rhizome that (Fig. 3.13 A) branches repeatedly and gives rise to sparingly branched aerial shoots Fig. 3.13A. The branching of the rhizome is usually dichotomous. The dichotomies are equal or sometimes unequal, and irregular due to occasional injuries. The aerial shoots usually show only one dichotomy. The aerial axis in ***T. forsteri*** is highly branched. They bear foliar appendages which are reduced and scale like at the base (Fig. 3.13 A) but become distinct leafy structures towards tip. These leaves or the foliar appendages are arranged in two rows of sub-opposite pairs in species with flattened aerial shoots e.g. ***T. lanceolata*** and ***T. tannensis.*** In ***T. vieillardi*** the aerial shoots

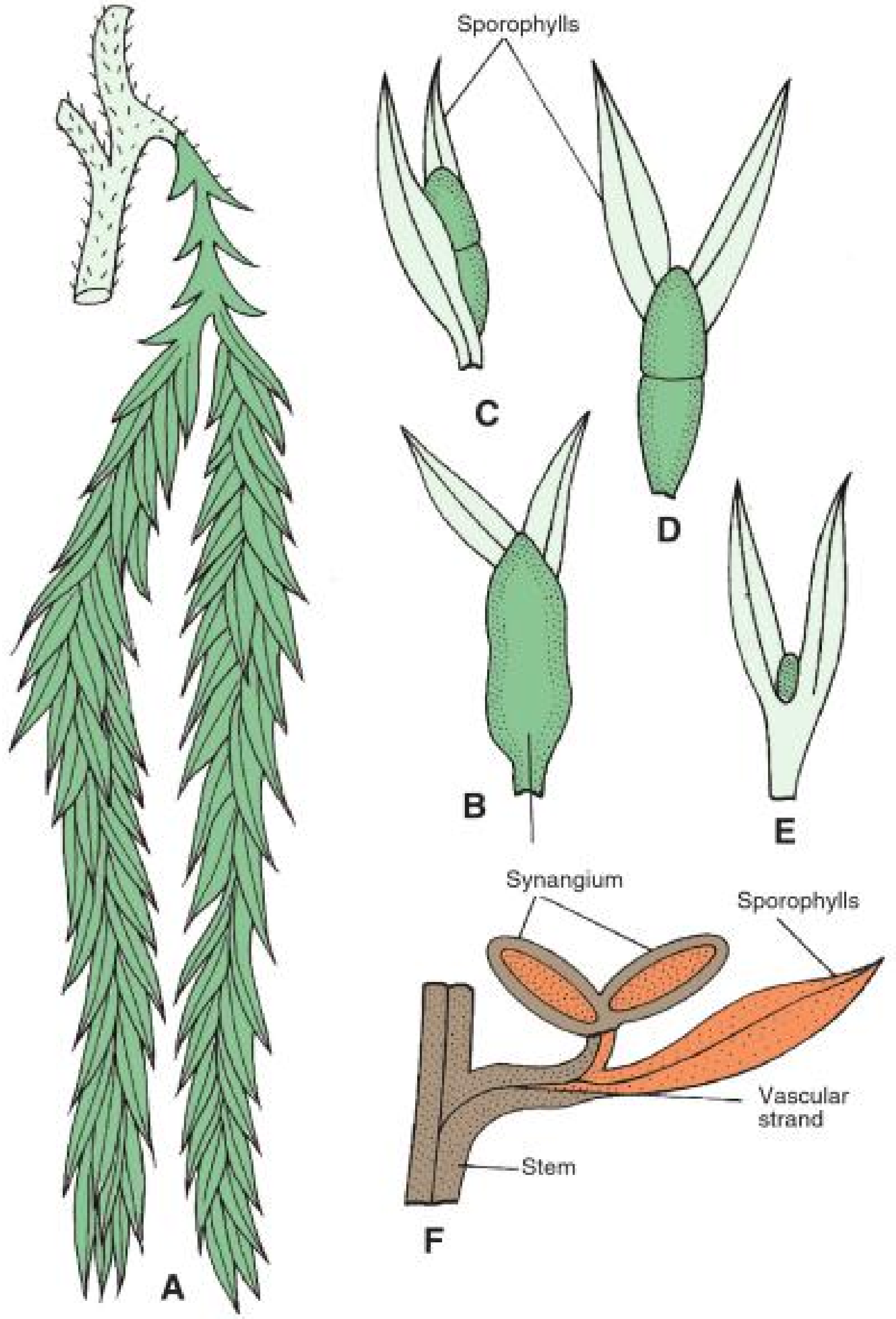


Fig. 3.13 (A–F). A complete sporophyte of ***T.tannensis*** showing habit; **B-F.** Fertile appendages as seen from different directions; **B.** from back; **C.** from side; **D.** from above; **E.** Adaxial view; **F.** Radial section showing vascular supply. (After Pritzel, F. After Eames)

have a radial symmetry and bear leaves in pseudospirals. The leaves are flat, lanceorlate and with a mucronate tip. They are about half an inch long. The smaller leaves at the base are **avascular** whereas the larger upper ones are traversed by a single distinct vascular strand. The leaf bases are continuous with the stem decurrent). The aerial shoot is terminated by a leaf.

The roots are absent and instead the rhizomes are covered with rhizoids that are evenly distributed all over the surface. The rhizoids may be unicellular or two to three cells in length. The rhizoids are covered by a cuticle.

The aerial shoots arise from the tips of rhizome. The tip turns up and grows into an aerial axis.

Anatomy of the Stem (Fig. 3.14 A-C)

A transverse section of the aerial stem reveals the following tissues from outside within:

Epidermis

It forms the outermost boundary of the stem and is composed of compactly arranged parenchymatous cells. A thick cuticle is present.

Cortex

It is composed of parenchymatous cells. In the aerial stems the parenchyma cells beneath the epidermis contain chloroplasts (Chlorenchymatous. Fig. 3.14 A-C). The chlorenchyma is absent in the rhizome and instead some cells with **collenchymatous** thickenings have been reported by Bierhorst (1971). The cells in the inner cortex contain brown tanniferous materials.

In the rhizome the innermost layer of the cortex is quite distinct as **endodermis** but in the aerial stems it is not so distinct. The last two or three layers of the cortex are often designated as endodermis and **pericycle.**

Vascular Region (Fig. 3.14 A–C)

The vascular region is a **protostele** (Fig. 3.14 C) in the basal region of the aerial shoot and the rhizome. In the flattened species (where stems are flattened) the stele in the basal region is U-shaped. The stele becomes a **siphonostele** (Fig. 3.14 B) in the aerial stems a little above the base. In this case a distinct pith appears in the centre and the xylem consists of five or more **protoxylem** groups surrounded by metaxylem. Near the apical parts of the aerial shoots the number of xylem groups decreases and they become irregularly arranged (Fig. 3.14. A) due to the departure of the leaf traces to the foliar appendages. The xylem consists of distinct protoxylem and metaxylem tracheids. The protoxylem elements range from **annular** to **helical** to occasional irregular forking among the systems of thickenings of the walls. The metaxylem elements, whem mature, show scalariform thickenings. Circular bordered pitting is also reported. The development of xylem is **mesarch** as compared to **exarch** development in ***Psilotum***.

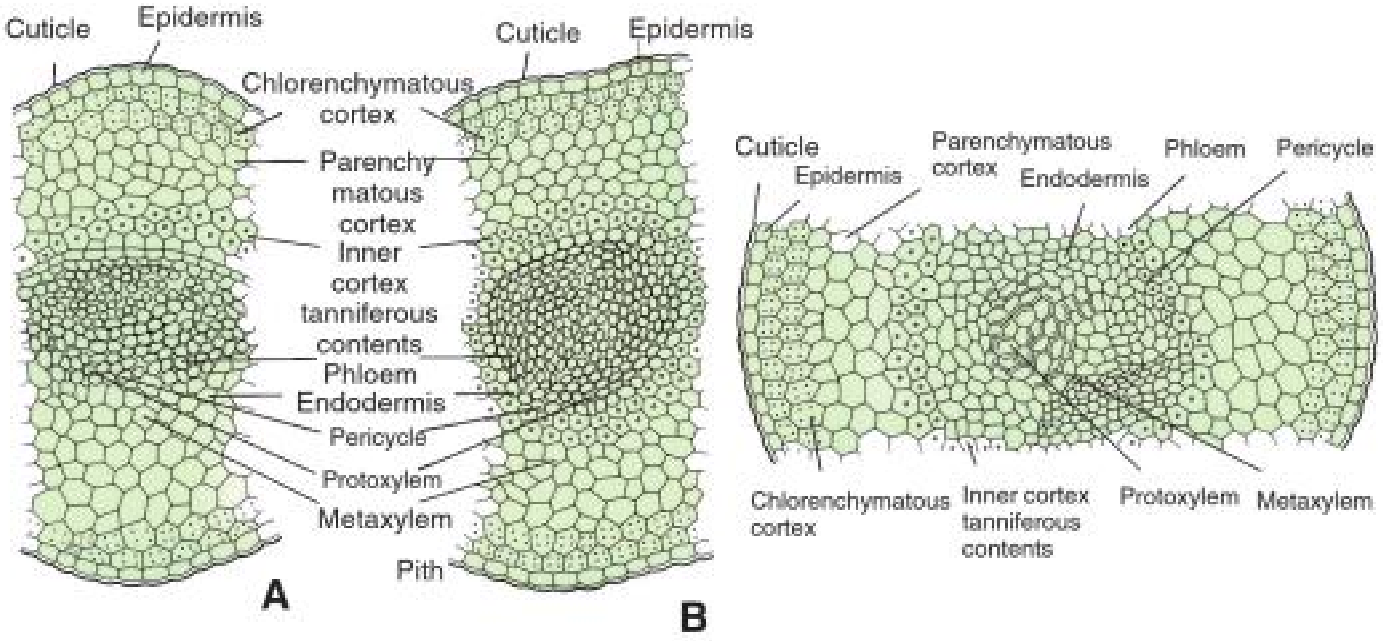

Cuticle
Epidermis
Cuticle
Epidermis
Chlorenchymatous cortex
Parenchymatous cortex
Inner cortex tanniferous contents
Phloem
Endodermis
Pericycle
Protoxylem
Metaxylem
Pith
A
B
Cuticle
Epidermis
Parenchymatous cortex
Endodermis
Phloem
Pericycle
Chlorenchymatous cortex
Inner cortex tanniferous contents
Protoxylem
Metaxylem

Fig. 3.14 (A–C). Transverse sections of the aerial shoot cut at various levels. **A.** T.S. near the apex showing irregularly arranged xylem groups; **B.** T.S. above the base showing a siphonostele with a distinct pith surrounded by xylem. Note the five protoxylem groups; **C.** T.S. at the base showing protostele with protoxylem in the centre (After Bower).

Phloem completely surrounds the xylem and consists of **sieve elements** with tapering end walls. The **sieve tubes** have numerous sieve areas on their lateral walls (Sykes, 1908).

Anatomy of the Leaf (Fig. 3.15)

The leaf in ***Tmesipteris*** shows a basal meristematic zone (intercalary meristem) which adds to its length. It grows in width by marginal meristematic activity. The terminal pinna in ***Tmesipteris*** develops directly from the apex of the aerial shoot, which is consumed in its formation.

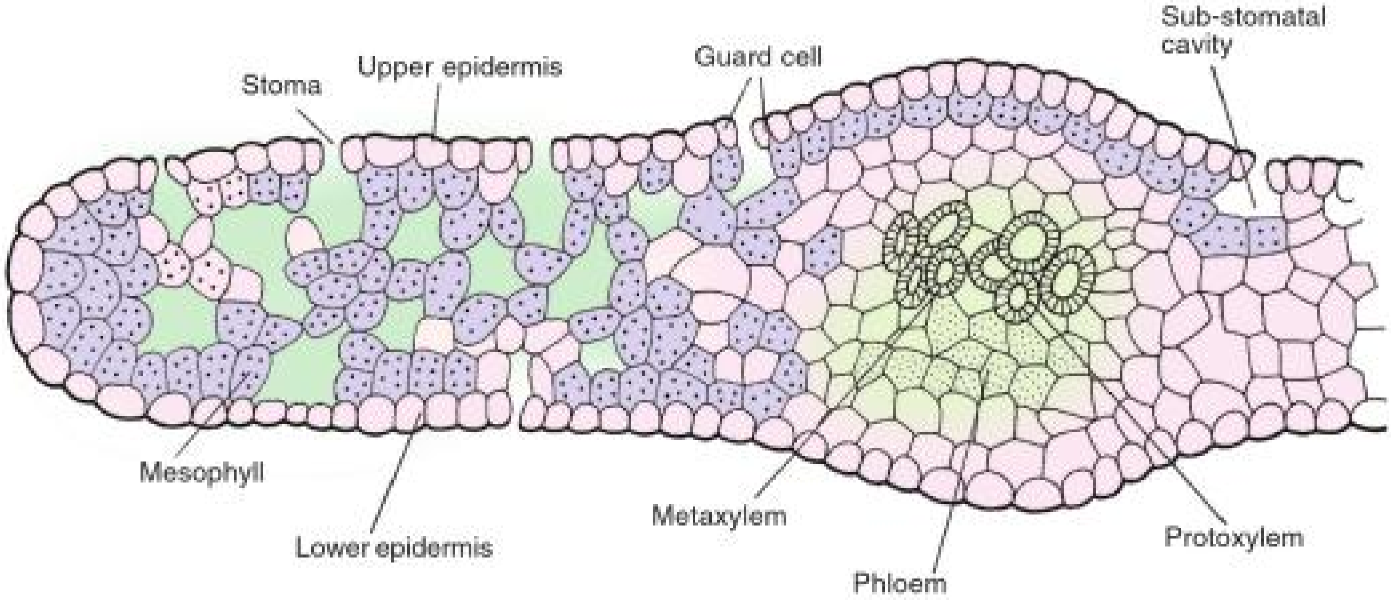


Fig. 3.15. *Tmesipteris tannensis.* V.S. through leaf (After Sykes)

The leaves in ***Tmesipteris*** are larger then those of ***Psilotum*** and show a comparatively well marked internal organisation. The leaves have distinct upper and lower epidermal layers. The epidermis is made up of a single layer of cells whose outer walls are cutinised. Stomata are present on both the epidermal surfaces. The region between the two epidermal layers is called **mesophyll** and is composed of lobed parenchyma cell that contain chloroplasts.

The single vascular strand is located in the centre and consists of several protoxylem tracheids surrounded incompletely by metaxylem elements. Phloem surrounds the xylem. No distinct endodermis is present.

The Fertile Appendages (Fig. 3.13. B-F)

The fertile appendages or the sporangia bearing structures which have been named as **fertile pinnae** by Bierhorst (because he designates the aerial shoots as fronds) and usually known as **sporophylls** are arranged in the same manners as the leaves. They can arise anywhere on the aerial axis. In ***Tmesipteris*** their position has been observed to vary with species. In ***T. lanceolata*** they arise near the base of the aerial shoot. In ***T. tannensis*** they arise at different places along the length of the aerial stem. In ***T.vieillardi*** they occur in the form of a strobiloid cluster at the tip of the stem.

Each sporophyll consists of a short lateral branch or the **fertile axis** (Fig. 3.13 F) terminating in a bilobed sporangium with two foliar appendages situated below the sporangium. These foliar appendages may grow more and extend beyond the sporangium. The vascular strand of the fertile axis divides into three strands just at the point where the foliar appendages arise. Out of the three strands two lateral ones enter the foliar appendages whereas the median one continues its course upwards and again divides into three strands. Two out of these supply the margins of the sporangium and the third enters the septum. The fertile axis arises laterally from the aerial stem and has also been called the sporangiophore. It takes the place of a sterile leaf.

Structure of the Sporangium (Fig. 3.16 C)

It is a bilobed structure that is more than two millimeters long. A section through the sporangium (Fig. 3.16 C) reveals that it is partitioned into two sporogenous regions (Fig. 3.17 C, D). The wall of the sporangium is made of three or four layers. There is no **tapetum.** In a mature sporangium there is, however, breakdown of inner wall layers. The inner wall layers extend inwards to form the septum between the two **sporogenous masses.** (Fig. 3.17 C). The sporogenous cells divide and some of them function as **spore mother cells** whereas the rest degenerate and form the nourishing fluid. The spore mother cells undergo meiosis to form tetrads of spores, that may be tetrahedral or even bilateral. At maturity the inner wall layers break down, whereas the cells of the outer layer become thickened. The dehiscence of the sporangium is **loculicidal.**

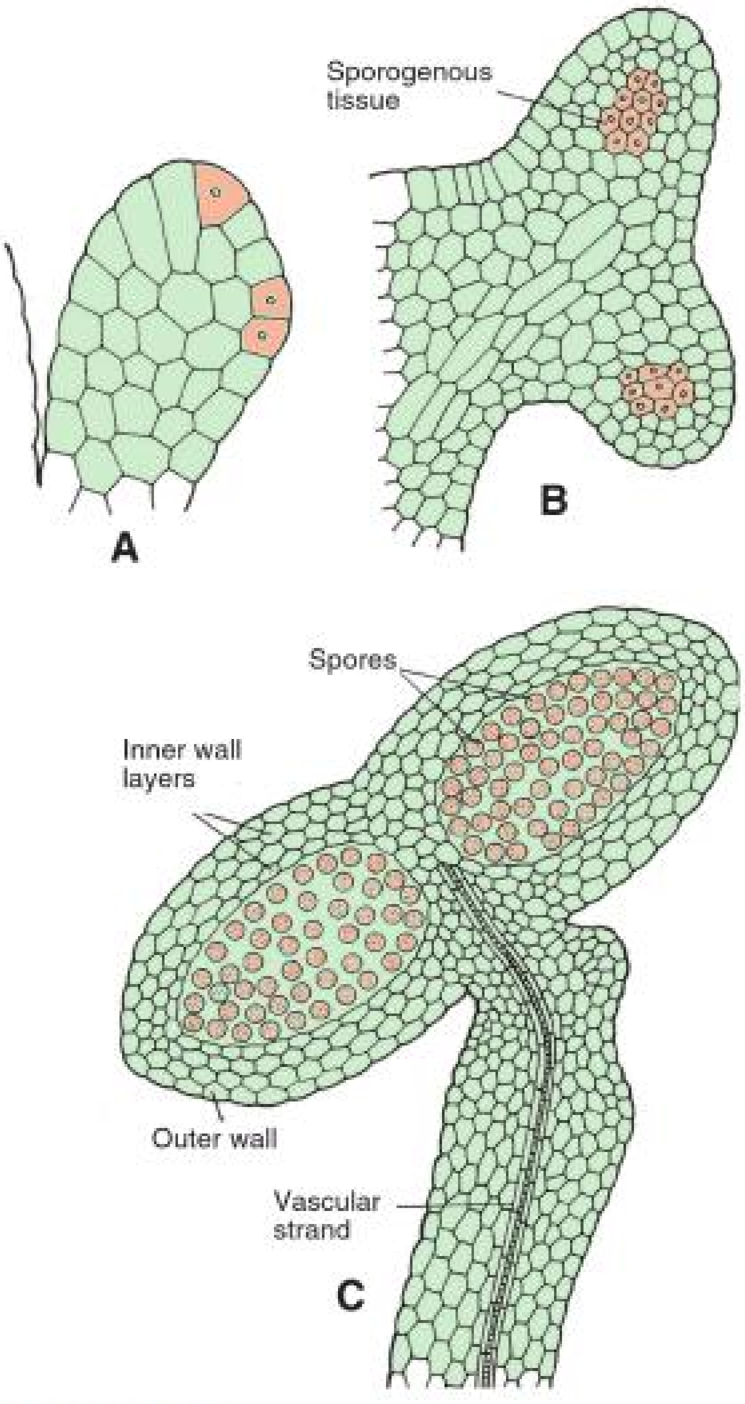


Fig. 3.16 (A–C) *T. tannensis.* **A.** A very young sporangium; **B.** a later stage in development; **C.** A mature synangium (A-B. after Bower, C. after Foster and Gifford).

Development of Sporangium (Fig. 3.16 A-C & Fig 3.17 A-D)

The development of sporangium is of **eusporangiate** type. The fertile axis grows by means of an apical cell (Fig. 3.17 A, B.) into a fertile axis. Two separate surface initials make their appearance at the apex of the fertile axis and indicate the sites of two sporangial locules. Each initial divides periclinally to form an outer **primary wall initial** and an inner **primary sporogenous initial** or cell. The former undergoes periclinal and anticlinal divisions to form a three or four layered thick sporangial wall. The primary sporogenous cell divides to form a mass of sporogenous cells (Fig. 3.16 B and 3.17 C). The sporogenous cells develop into **spore mother cells** which undergo meiosis to form tetrads of spores. Some of the sporogenous cells may disintegrate to form nourishing fluid. The leaf like appendages at the base of the sporangium develop later and usually overgrow the sporangium (Fig. 3.13 B-F).

Morphology of the Sporangial Stalk

Regarding the nature of the sporangial stalk various views have been put forth. These can be summarised as below :

1. Miss Sykes (1908), regards the sporangium as axial in position. This view is supported by the presence of a vascular bundle.

2. Sahni (1925) regards the sporangiophore as a shoot structure.
3. In 1921 Miss Margret Bensen explained that the sporangiophore of ***Tmesipteris*** is an axial structure and the two lobes are cladodified branches of the axis.
4. One view holds that the leaf is also a modified branch of the aerial system. It is possible that sometimes the leaf may have preceded the specialised sporangiophore in its differentiation.

The discovery of Rhyniaceae, in which the sporangium is not an organ by itself, but the modified end of a branch, seems to support the view that the sporangiophore is a fertile branch.

The structure of the spore is similar to that of ***Psilotum***. It germinates into a prothallus or gametophyte. The stages of germination are not known.

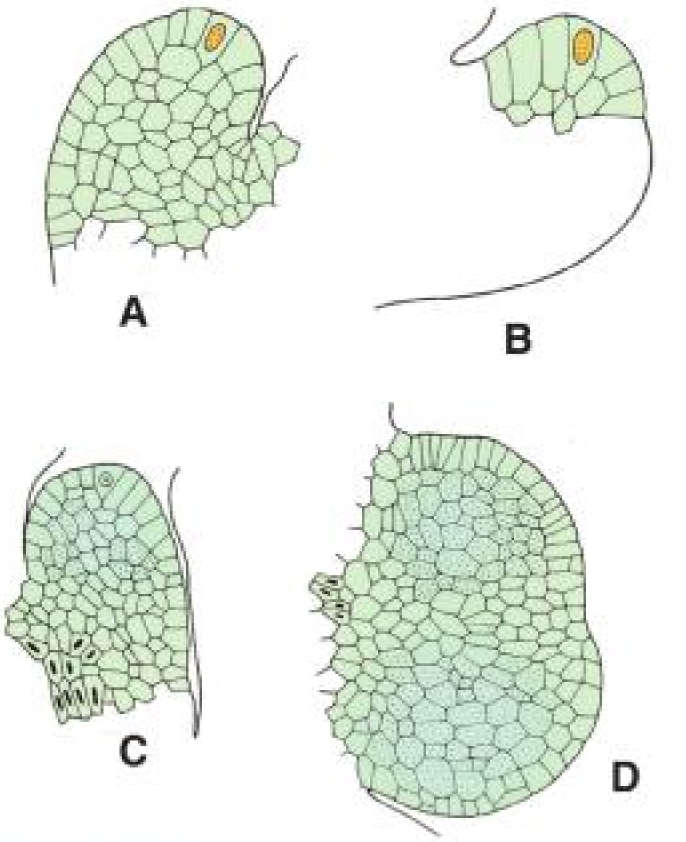


Fig. 3.17 (A–D). *T. tannensis.* **A-B.** Young fertile appendages with apical cells; **C-D** Synangia in later stages of development (After Bierhorst)

Gametophyte (Fig. 3.18 A-D)

The prothallus of ***Tmesipteris*** is subterranean. It is found usually in moist, sandy soil and is deviod of chlorophyll. Its mode of nutrition is saprophytic. It varies in form and may be cylindrical, bent, curved and sometimes twisted in curious forms. It is branched and each branch is provided with an apical meristem. Numerous rhizoids arise from its surface. The rhizoids are long and unicellular and afford immense absorptive surface.

The presence of endophytic fungus (***Chladochitrum tmesipterides***) is necessary for the development of the prothallus. There is a distinct epidermal layer composed of slightly thickened cells that are sharply defined. The rest of the tissue is uniform throughout. There is no differentiation into vegetative and reproductive regions. A more distinct pattern of distribution of gamentangia (sex organs) is seen in a species of ***Tmesipteris*** from New Caledonia where they occur in distinct zones along the axis. The surface cells within the fertile zones are relatively shorter than those in the infertile areas.

Sex Organs (Fig. 3.19 and 3.20)

They are distributed all over the surface of the prothallus.

Antheridium (Fig. 3.19). The antheridia are distributed all over the surface of the prothallus and are invariably accompanied by archegonia. The antheridium is larger in size than the archegonium. It is almost spherical in shape and is almost completely above the epidermal surface. A mature antheridium is composed of an outer wall one cell in thickness. The antheridial wall encloses a mass of spermatogenous cells which number 128-512. The contents of these cells metamorphose into multiciliated spermatozoids. The jacket has a single opercular cell that breaks down to allow exit of spermatozoids.

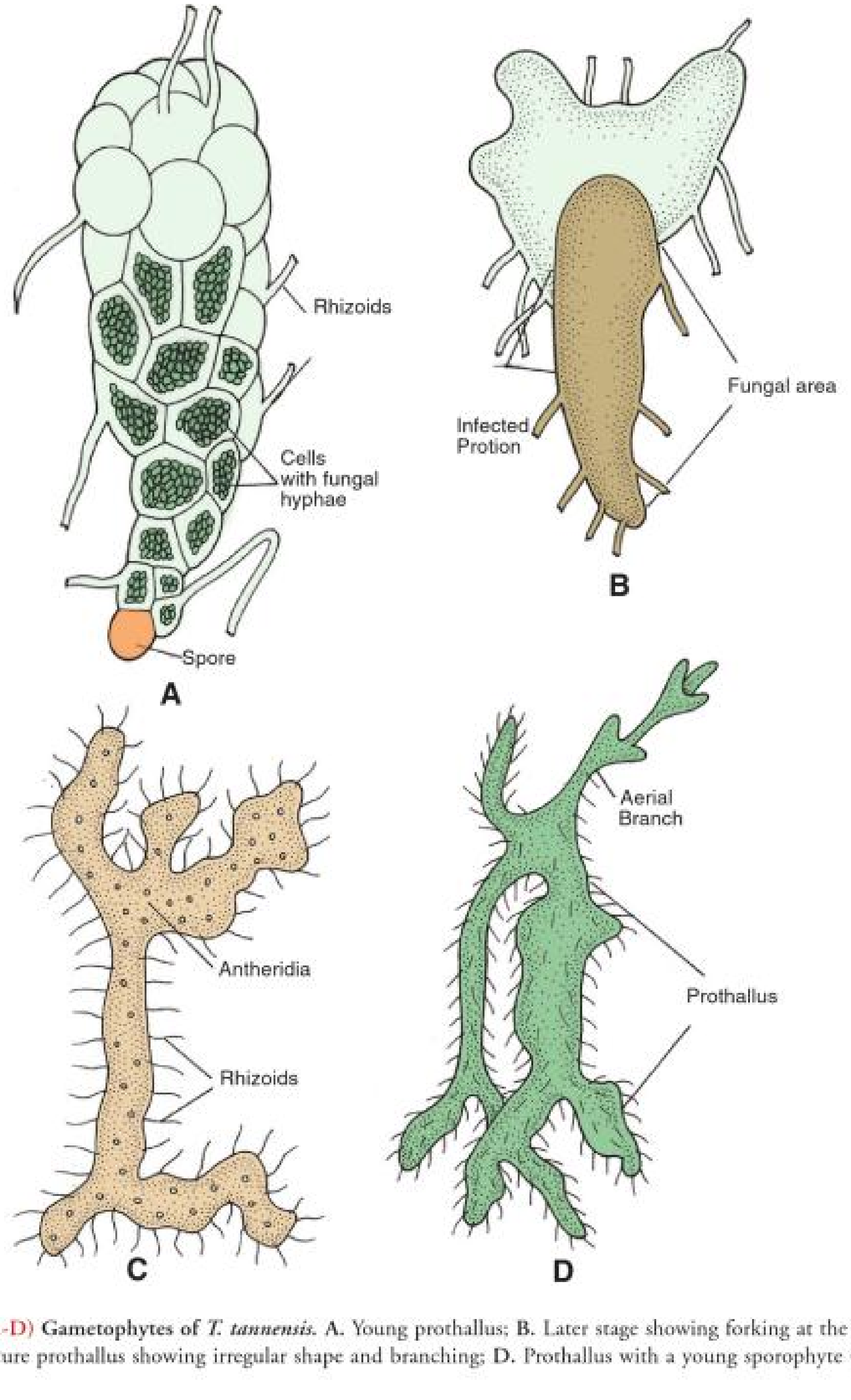

Rhizoids
Cells
with fungal
hyphae
Spore
A
Infected
Protion
Fungal area
B
Antheridia
Rhizoids
C
Aerial
Branch
Prothallus
D

Fig. 3.18 (A-D) **Gametophytes of *T. tannensis.*** **A.** Young prothallus; **B.** Later stage showing forking at the distal end; **C.** Mature prothallus showing irregular shape and branching; **D.** Prothallus with a young sporophyte (After Holloway).

The antheridium develops (Fig. 3.19. A) from a single superficial cell that divides periclinally into an outer **jacket initial** and inner **spermatogenous** ***cell.*** The nucleus of the spermatogenous cell undergoes division and contains several free nuclei. Meanwhile the jacket initial divides by anticlinal wall formation to give rise to a single layered jacket. Delicate walls are then laid around the free nuclei in the spermatogenous cell to form a spermatogenous tissue. They divide further to form **sperm mother cells** whose granular contents and larger nuclei distinguish them from other cells. At this stage the antheridium assumes a spherical shape and enlarges in sieze. The nuclei undergo change and appear dense, coiled and crescent shaped bodies. They metamorphose into multi-ciliated and coiled **spermatozoids** (Fig. 3.19 E).

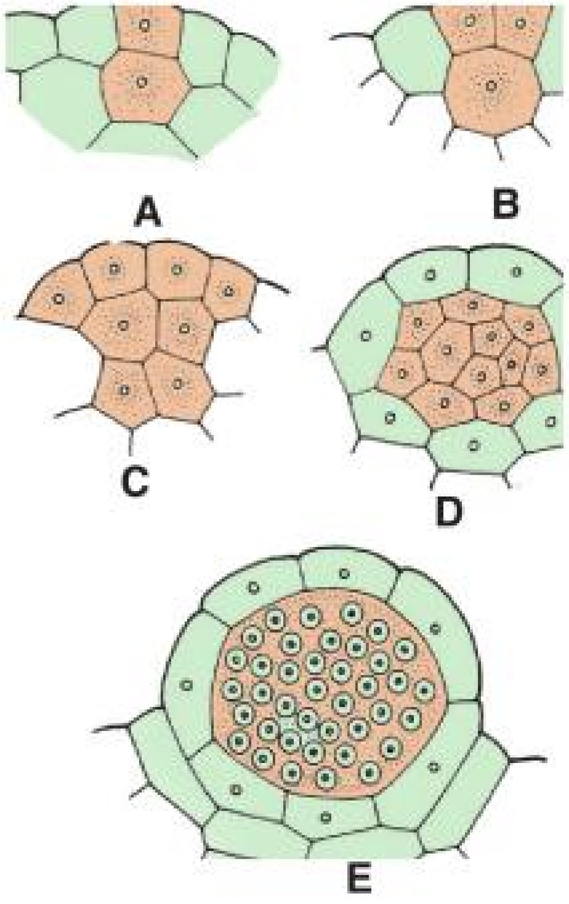


Fig. 3.19 (A-E). Various stages in the development of an antheridium in *T. tannensis* (After Holloway)

Archegonia (Fig. 3.20)

Their size is comparatively smaller than the antheridia and are produced in larger numbers. The archegonium neck is made up of 4 longitudinal rows of cells that project above the surface of the prothallus. The venter remains embedded in the tissue of the prothallus. Each row of the neck is 4 celled high ***i.e***. the neck consists of four tiers of four cells each. The venter contains the egg cell. The neck encloses a neck canal which contains two nuclei.

The archegonium develops from a superficial cell of the prothallus. It enlarges in size and divides by a periclinal wall into an outer **cover cell** and an inner **central cell.** The cover cell divides twice anticlinally and then by a series of periclinal walls to form an archegonial neck made up of four tiers of four cells each. The neck protrudes above the surface. The central cell divides periclinally into a lower **primary ventral cell** and an upper **primary neck canal cell.** The former divides into an **egg cell** and a **ventral canal cell.** The primary neck canal cell nucleus divides into two neck canal nuclei. No wall is laid down between them.

At maturity the upper three tiers of the neck disorganise (Fig. 3.20. C), the fourth tier forming a flat disc, slightly concave in the middle, but otherwise quite parallel with the surface of the prothallus. This results in the great shortening of the neck at the time of fertilisation. This is an adaptation to meet the unusual condition of subterranean fertilisation.

As soon as the antheridium dehisces, the spermatozoids come out in the surrounding thin film of moisture. They swim towards the archegonia presumably attracted by some chemical substance. They enter the open neck and one of them reaches the egg to effect fertilisation. After fertilisation the zygote is completely enclosed in the venter by the formation of calyptra (Fig. 3.21A).

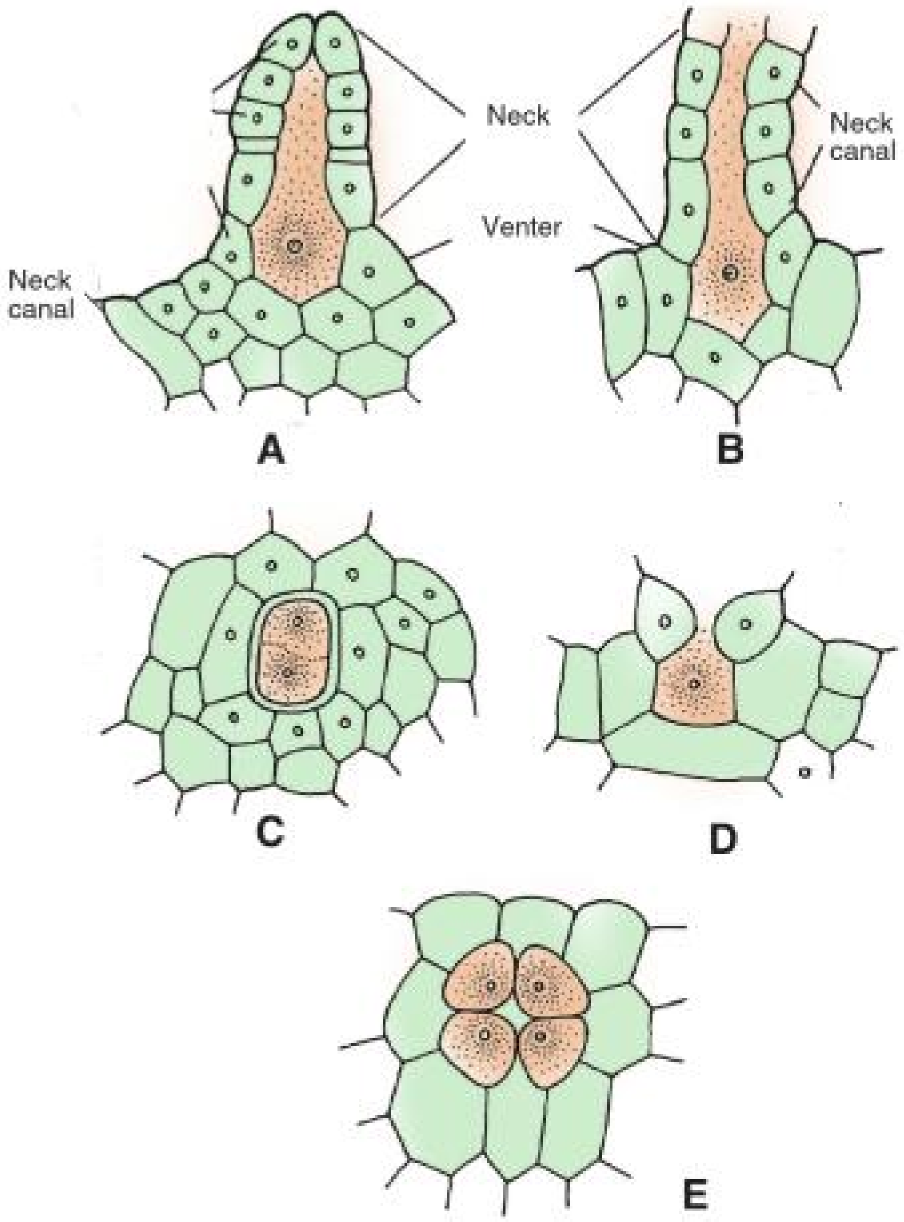


Fig. 3.20 (A-E) *T. tannensis* Archegonium. **A.** Mature archegonium (After Holloway); **B.** Mature archegonium (After Lawson); **C.** Archegonium after fertilisation when the projecting part of the neck has been shed (After Holloway); **D.** Same as C (After Lawson); **E.** Archegonium as viewed from surface during fertilization (After Lawson)

Embryogeny (Fig. 3.21 A-D and 3.22 A-E)

The development of embryo is known only for ***T. tannensis.*** The zygote elongates (Fig.3.21 A) and then divides by a transverse wall (Fig. 3.22, A) into an **epibasal cell** (towards the archegonial neck) and a **hypobasal cell** (Fig. 3.22 A). The hypobasal cell divides repeatedly to from the **foot** whereas the epibasal cell divides repeatedly to form the sporophyte axis. After a few divisions of the epibasal cell two growing points or apical cells (Fig 3.22, D) are established at the flanks. The establishment of two apical cells result in the formation of a branched rhizome (Fig. 3.23 A, B). In the foot region further divisions lead to the formation of lobed structures that extend into the gametophyte tissue (Fig. 3.21, D and Fig. 3.22 D, E). In the epibasal region the two apical cells divide while still contained in the gametophyte tissue. Later they emerge out of the calyptra and branch into two. The branched rhizome is subterranean. In ***Tmesipteris*** it develops into green aerial shoots quite early as compared to ***Psilotum*** where green aerial parts arise quite late, may be after several years.

The embryology in ***Tmesipteris*** is **exoscopic.** The young sporophyte of ***Tmesipteris*** (Fig.3.21 D, 3.22 E) appears to be quite similar to that of ***Anthoceros*** in possessing a haustorial foot.

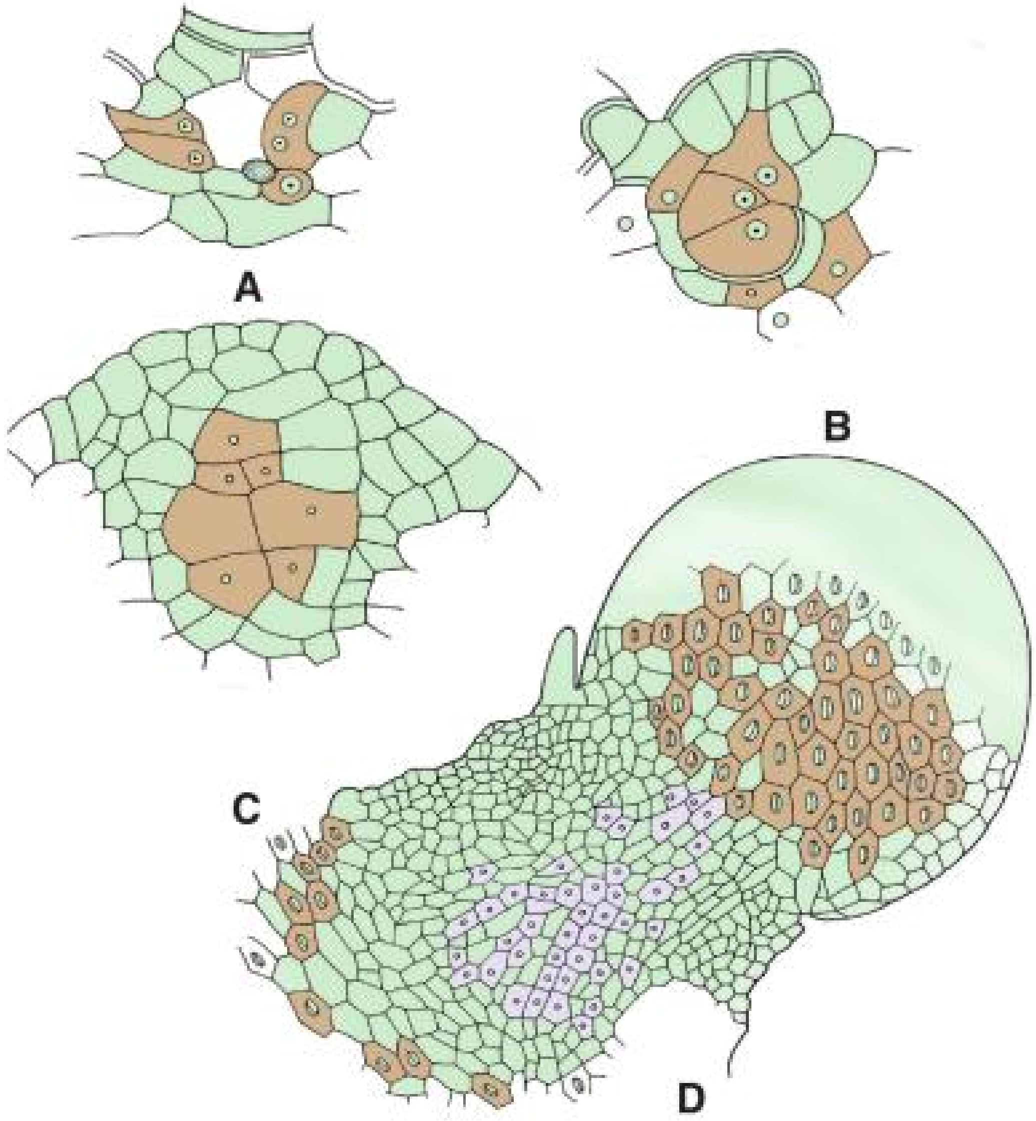


Fig. 3.21 **(A-D)** *T. tannensis.* **A-C.** Earlier stages in the development of embryo; **D.** Mature embryo showing lobed foot, the central strand and surrounding tissue (After Holloway).

Chromosome Number

Barber (1957) in his article Polyploidy in Psilotales' has mentioned the Chromosome numbers in ***Tmesipteris tannensis*** as $n = 200+$. He recognised six new species of ***Tmesipteris***, five out of which have $\boldsymbol{n} = 204 – 210$ and one has $n = 102–105$. The basic chromosome number for the family is considered to be $x = 13$ (Chiarugi, 1960, Ninan, 1956).

Taxonomic Position

Division : *PSILOPHYTA*
Class : *PSILOTOPSIDA*
Order : *PSILOTALES*
Family : *PSILOTACEAE*
Genera : *Psilotum* and *Tmesipteris*

Psilotum and Tmesipteris Compared

Resemblances

The two genera resemble each other in the following respects :—

1. Both may grow in soil or as epiphytes.

2. The plant body in both is distinguished into a lower subterranean rhizome which gives rise to aerial axis.
3. In both aerial branches grow from rhizome apices.
4. The rhizome bears numerous multicellular rhizoids.
5. The foliar appendages in both are arranged in spirals or pseudo-spirals or sometimes just-opposite.
6. The anatomy of stem in both is similar in many respects.
7. The development and structure of the sporangium is similar in both the genera except some minor differences.
8. The prothallus in both is subterranean and saprophytic. It is covered with numerous rhizoids.
9. The structure and development of sex organs in both is similar.
10. The development of embryo in both is similar to a greater extent.
11. The basic chromosome number in both is believed to be $x = 13$.
12. Polypoidy is prevalent in both the genera.

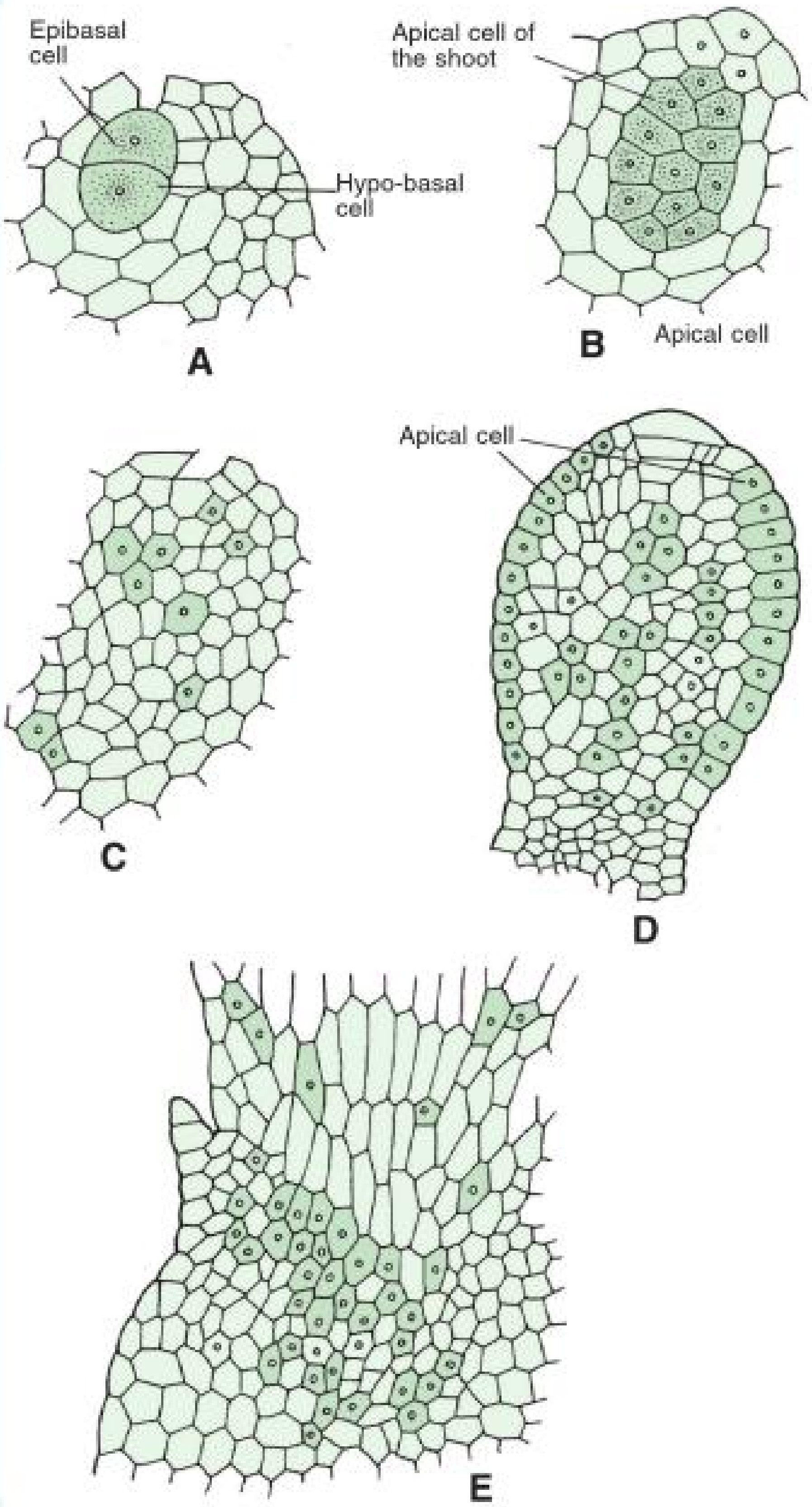


Fig. 3.22 (A–E) *T. tannensis* Embryology **A.** Two celled embryo with an epibasal and a hypobasal cell; **B.** Embryo with a distinct apical cell of the shoot; **C.** The epibasal cell has produced an irregular lower part that will develop into a foot; **D.** Young embryo showing lower foot and the epibasal hemisphere with apical initials that will grow into a shoot; **E.** Basal portion of the mature embryo showing a lobed foot. (After Holloway)

Differences

Tmesipteris	*Psilotum*
1. The aerial branches are sparingly branched and show only one dichotomy.	The aerial shoots are profusely branched and show repeated dichotomy.
2. The foliar appendages are larger in size, green, and possess a distinct single vein in the centre.	The foliar appendges are minute and **avascular.**
3. Stomata are present in the leaves.	The stomata are absent.
4. The xylem development is **mesarch.**	The xylem development is **exarch.**
5. The xylem is not star-shaped but consists of varying number of xylem groups near the apex, it is a siphonostele in the middle and the xylem is U-shaped or a protostele at the base.	The xylem is star-shaped and is usually a protestele and not siphonostelic.
6. The sporangium is bilobed.	The sporangium is trilobed.
7. The tapetal layer is absent.	The tapetum is present.
8. Two foliar appendages are associated with the sporangium.	Only one bilobed foliar appendage is associated with the sporangium.
9. The lateral fertile axis that bears the Sporangium and foliar appendages is long and distinct.	The fertile axis is abbreviated.
10. The prothallus is smaller in size, thin and dark brown.	The prothallus is comparatively larger in size and is thicker.
11. The prothallus is wholly subterranean.	The prothallus may be wholly or even partially subterranean. It projects out slightly from the crevices in the rocks.
12. The antheridia are much more numerous than the archegonia.	The archegonia are numerous than the antheridia.
13. The archegonia occur in dense crowded groups.	The archegonia are widely separated from each other.
14. The antheridia and archegonia are larger in size.	The antheridia and archegonia are comparatively smaller in size.
15. The zygote enlarges sufficiently before dividing.	The zygote does not show much enlargement.
16. The embryonic shoot possesses two apical cells.	The embryonic shoot possesses only one apical cell.
17. The aerial shoots arise early from the embryonic shoot.	The aerial shoot sometimes takes several years to develop from the young subterranean rhizome.
18. The aerial shoot is terminated by a leaf.	The aerial shoot is not terminated by a leaf.

Distinct Features of the Prothallus

1. The gametophytes of the Psilotaceae are subterranean. **2.** The colour is light brown or dark brown. **3.** They lack chlorophyll. **4.** The body is usually cylindrical. It branches and each branch has a terminal meristem. **5.** The prothallus tissue is uniform except the epidermal layer that is quite distinct. **6.** Presence of tracheidal cells or even distinct vascular strands is a unique feature of the Psilotaceous gametophyte. **7.** The prothallus is saprohytic and is attacked by an endophytic fungus. **8.** Surface of the prothallus is beset with numerous unicellular rhizoids. **9.** The prothallus is monoecious. **10.** The sex organs are irregularly distributed and intermingled. **11.** The spermatozoids are multiflagellated. **12.** The antheridia bulge above the surface of the prothallus. **13.** The archegonial neck is composed of four longitudinal rows of cells and projects above the surface of thallus. The venter is embedded. **14.** Disorganisation of the tiers of neck cells is a common feature.

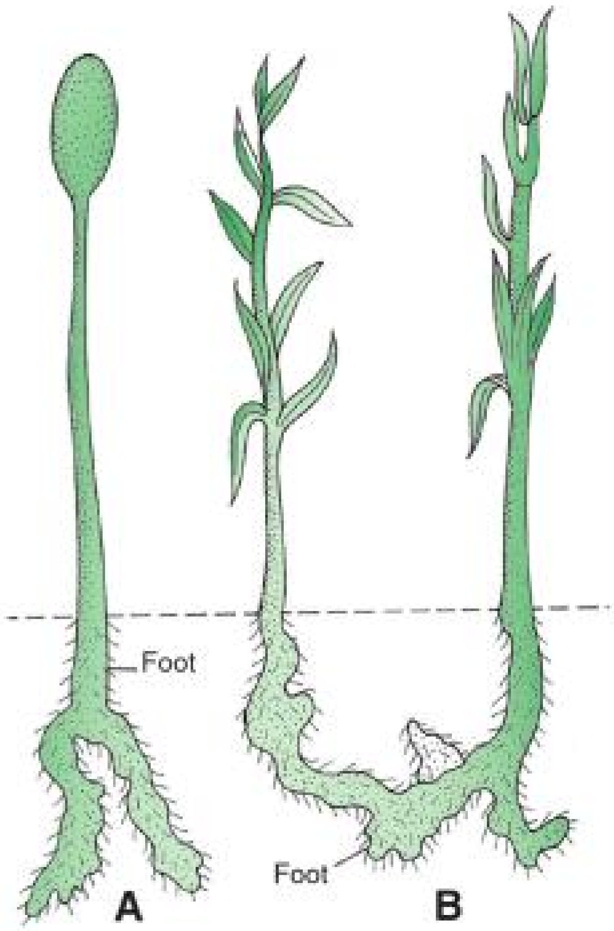


Fig. 3.23 **(A-B).** Young sporophytes of *T. tannensis* **A.** Only one of the embryo apices has grown into a young shoot; **B.** Both the apices of the embryo have grown into two young plants. (After Holloway)

Affinities of Psilotales

Regarding the affinities of this group there are still doubts in the minds of botanists. Four theories have been put forth to explain the position of the group :

1. Kidston and Lang (1917–1921) propounded a theory suggesting close relationship between Psilotales and Psilophytales. This theory is also supported by Holloway and Bower.
2. Arber suggested their late origin along independent lines from the algae.
3. The hypothesis maintained by A.P.W. Thomas and formerly suggested by Bower and Scott, of an affinity with the Sphenophyllales.
4. The old fashioned view that Psilotales are essentially Lycopods (Lawson, 1917).

Considering the first theory, the Psilotales resemble the Psilophytales in : (*i*) having rootless rhizomess, (*ii*) protostelic stem, (*iii*) small size of the leaves, and (*iv*) dichotomously branched shoots.

They differ only in the position and number of sporangia. Kidston and Lang pointed out that not only do the Psilotales resemble the fossil Psilophytales in vegetative characters, but that even in the fructifications a reliable basis for comparison is supplied by the repeatedly forked aerial shoots of Rhyniaceae with their large terminal sporangia capable of showing the dichotomy of the axis (***Horneophyton***). Considering the similarity of the various genera in the two orders, one might speculate that the present members of the Psilotales are living remnants of Devonian flora that has come down to the present day without much chang from the very ancient times.

Lawson (1917) expreses himself favourably towards the affinity with the Sphenophyllales while pointing out that the gametophyte generation can offer no positive evidence.

Affinity with Sphenophyllales is ruled out because there are many important differences between them and the Psilotales. The leaves in Sphenophyllales are whorled as compared to spiral arrangement in the Psilotales. The branching in the Sphenophyllales is monopodial as compared to the dichotomous branching in the Psilotales.

Regarding their affinities with the Lycopods as suggested by Lawson in 1917, after studying the gametophytic generations of the Psilotales, there seems no justification because of some major differences between their prothalli. Apart from some superficial resemblances like their subterranean existence, presence of mycorrhiza and absence of chlorophyll, there are striking differences also. The Psilotaceous prothallus does not show any tissue differentiation so characteristic of the Lycopods. The antheridia in the Psilotales are so prominently bulged out whereas in Lycopods they are completely embedded in the prothallus. The spermatozoids are multiflagellate in the Psillatales.

Arber agrees with Thoday and others in that the Psilotales are an entirely distinct group from either the Lycopods or the Sphenophyllales. Arber regards it as quite an independent race that had an algal ancestor.

Tmesipteris

Bierhorst (1968, 1969, 1970) has related ***Psilotales*** (Psilotaceae) to some filicalean families like ***Schizaeaceae*** and newly created ***Stromatopteridaceae***, which is a segregate from ***Gleicheniaceae***. He has included the family ***Psilotaceae*** (***Psilotum*** and ***Tmesipteris***) under the order ***Filicales*** and has placed it next to ***Stromatopteridaceae***. Such a conclusion has been drawn as a result of following similarities between the two families (Bierhorst, 1968) :—

1. The axial gametophytes are underground. **2.** The under ground sporophytic stem and the gametophytes are indistinguishable in both. **3.** The gametophytes bear septate rhizoids in both. **4.** Alternate periods of growth in both the sporophyte and the gametophyte produce short and long cell. **5.** The archegonia in both the families dehisce by the decapitation of the neck. **6.** The embryos are rootless. **7.** Spores are monolete. **8.** Similarities in the development and wall structure of the sporangia. **9.** The terminal leaf of ***Tmesipteris*** and terminal pinna of ***Stromatapteris*** develop from the apical meristem and consume it. **10.** Large superficial antheridia with lateral opercular cell which breaks down at maturity. Discontinuous vascular tissue in smaller axes of the sporophyte. **11.** Synchronous xylem maturation in smaller subterranean stems. **12.** Mesarch xylem without protoxylem elements in the large subterranean stems. **13.** Successive dichotomies with determinate apices in the vertical subterranean stem system. **14.** A laxity of chromosome coiling at meiosis so that chromosomes in anaphase resemble early prophase ones. **15.** Nucleoli at mitosis persist up to anaphase stage.

Significance and Phylogeny of Psilophyta

The affinities of the two classes of Psilophyta have been discussed in detail in the relevant chapters. The division Psilophyta is of great evolutionary significance as it includes two closely related classes of extinct and living plants (Psilophytopsida and Psilotopsida). They are the oldest known and simple vascular plants that possess no roots and are either leafless or possess rudimentary leaves. They have been regarded as connecting links between the aquatic algae and the terrestrial and more complex vascular plants like the lycopods, horsetails, and the ferns. Some Psilophytales resemble some algae in (*a*) their dichotomously branched axes ; (*b*) absence of leaves ; and (*c*) absence of roots. They differ from algae in possessing : (*a*) definite cuticle ; (*b*) stomata ; (*c*) cutinised spores ; and (*d*) a vascular system with well defined xylem and phloem.

This division of plants offers a number of evidences that have a great evolutionary importance. These can be listed as below :

1. They throw light on the origin of root, as suggested by Prof. Lignier from that portion of the axis which became negatively geotropic and entered the soil where it became adapted to perform the functions of anchorage and absorption. The rootless and subterranean rhizomes of the Psilophytales and Psilotales offer a great support to this because they grow beneath the surface of the soil and serve to fix the plant and absorb nutrition.
2. They also suggest the origin of microphyllous and megaphyllous leaves of lycopods and ferns. The leaf-like emergences of ***Asteroxylon*** and ***Psilotum*** might have developed into small single veined and microphyllous leaves of the Lycopods. In ***Pseudosporochnus*** and ***Protopteridium***, the leaves are formed by flattening of the branch system and are supposed to have led to the development of larger and megaphyllous leaves of ferns.
3. The anatomy of the shoot in the Psilophytales also suggests that protostele is the primitive type of vasculature and that siphonostele has originated from it by the appearance of pith. It also suggests that annular tracheids are the simplest and the spiral and scalariform tracheids are advanced.
4. A comparative study of the Psilophytales and the higher vascular plants also suggests the establishment of four distinct subdivisions, namely, the Psilopsida, Lycopsida, Sphenopsida and the Pteropsida. The Psilophytales indicate clearly the three lines of evolution which lead to the development of Lycopsida, Sphenopsida and the Pteropsida.

Psilophytales= *Protopteridium*

Certain members of the Psilophytales, ***e.g.***, ***Asteroxylon*** possess small leaves that arise as emergences and might have given rise to the Lycopsid line of development.

A few Psilophytales, ***e.g.***, ***Pseudosporochnus*** and ***Protopteridium*** exhibit a tendency towards the formation of leaves by the flattening and webbing of branch system and might have led to the development of large leaved vascular plants or the Pteropsida.

This line of evidence, therefore, suggests that the plants with microphyllous and megaphyllous leaves had separate lines of evolution. It suggests that the old division pteridophyta should be split up at least into two subdivisions, the Lycopsida and Pteropsida. The seed plants are included in the Pteropsida, along with the ferns, because they have megaphyllous leaves. The ferns are closer to the seed plants (spermatophyta) than to the Lycopsida and the Sphenopsida.

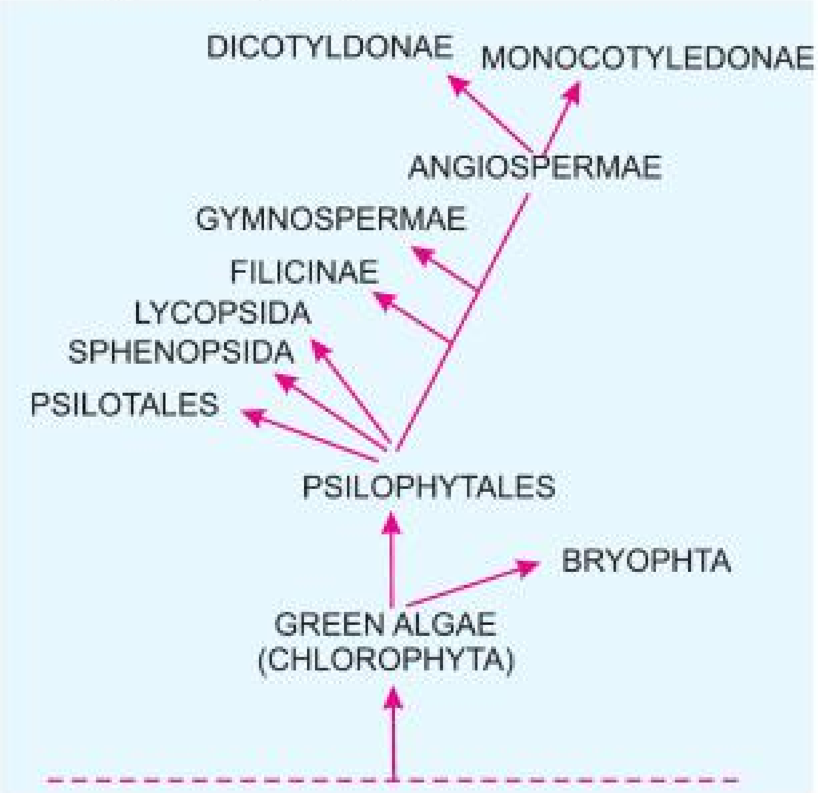


Fig. 3.24. Phylogenetic scheme illustrating relationship among various groups of vascular plants (After Fuller and Tippo)

The above evidences lead us to conclude that the Psilophytales have originated from the green algae and have in turn given rise to the three subdivisions of the vascular plants, namely, the Lycopsida, Sphenopsida and the Pteropsida. It is also believed that the bryophyta have also originated from the green algae and have followed a different course of evolution that has ended blindly. It is also believed by some botanists that bryophytes may have originated as a result of retrogresive evolution accompanied by reduction, from the Psilophytales.

The Psilotales are regarded as the last living descendants of the Psilophytales. They have persisted through ages unchanged and have retained in a remarkable manner their simple structure. They have been aptly regarded as the 'living fossils'.

Fuller and Tippo have drawn out a scheme (Fig. 3.24) of phylogenetic relationship among the various groups of vascular plants.

CHROMOSOME NUMBERS :— The haploid chromosome number in ***P. nudum*** has been reported to be $n = 50$ (Rosen, 1896) or $n = 52$ (Okabe 1929). Diploid prothalli with $n = 100$ (Manton, 1950), 104 (Barber 1957, Sorse 1965, Walker, 1965, Ninan 1956, 1965) have also been reported from various localities in India and abroad. Brownlie (1965) reported $n = 210$ in ***P. nudum*** from New Caledonia. Sinha and Verma (1971) reported $2n = 312$ in a hexaploid ***P.nudum*** from Patna. The same authors reported (1978) $2n = 468$ from Patna.

QUESTIONS

ESSAY TYPE

1. Describe the chief characteristics of ***Psilotum*** and discuss the phylogeny of Psilotales in the light of recent researches.
2. Describe the distinguishing features of Psilotales. What is the structure of Synangium? Discuss the distribution of ***Psilotum***.
3. Justify the creation of two distinct monotypic families of Psilotopsida.
4. Give a comparative account of the gametophytes of ***Psilotum***, ***Lycopodium*** and ***Ophioglossum***.
5. Where ***Psilotum*** is found in India? Mention the salient features of ***Psilotales*** and discuss its systematic position.
6. Discuss the primitive characters of ***Psilotum***.
7. Describe the life history of ***Psilotum*** and pointout the features of its primitiveness.
8. "***Psilotum*** combines the characters of simplicity and primitiveness". Discuss.
9. Describe the structure of synangium of ***Psilotum*** with the help of a suitable diagram and comment on its morphology.
10. Describe the synangium of ***Psilotum***.
11. Give an account of stelar structure of ***Psilotum*** and comment on the affinities of the genus.
12. Give a comparative account of the spore producing organs of ***Psilotum***, ***Selaginella*** and ***Equisetum***. **(Kerala, 2001)**
13. Describe the external and internal structure of ***Psilotum*** stem. **(Bangalore, 2001)**
14. Give an illustrated account of asexual and sexual reproduction in ***Psilotum*** or ***Tmesipteris***.
15. With the help of labelled diagrams give an account of the Sporophyte of ***Tmesipteres***.
16. Describe the life-history of ***Tmesipteris***.
17. Describe the structure of prothallus in ***Tmesipteris***.
18. Give an illustrated account of the structure and morphology of sporangium of ***Tmesipteris***.

SHORT ANSWER TYPE

19. Classify the following and write their salient features :
    (*a*) ***Psilotum***.
    (*b*) ***Tmesipteris***.
    (Awadh, M.Sc. 2000)
20. Write short notes on.
    (*a*) ***Psilotum***.
    (*b*) Prothallus of ***Tmesipteris***.
    (*c*) Development of synangium in ***Psilotum***. **(Kanpur, M.Sc. 2000)**
    (*d*) Aerial shoot of ***Tmesipteris***.

(*e*) Synangium in ***Psilotum***.

(Gauhati, 2000, 2002).

(*f*) Rhizome in ***Tmesipteris***.

(*g*) External morphology of ***Psilotum***.

(*h*) Stele of the aerial shoot of ***Psilotum***.

(*i*) Vascular bundle in ***Psilotum***.

(*j*) ***Prothallus*** of ***Psilotum***.

(Nagpur, 2002; Bangalore, 2001)

(*k*) Vegetative reproduction in ***Psilotum***.

(*l*) External morphology of ***Tmesipteris***.

21. Draw a labelled diagram of the following ;

(*a*) T. S. stem of ***Psilotum***.

(*b*) Synangium.

(*c*) T. S. aerial shoot of ***Psilotum nudum***.

(*d*) T. S. leaf in ***Psilotum***.

(*e*) T. S. aerial shoot of ***Tmesipteris***.

(*f*) Prothallus of ***Psilotum*** and ***Tmesipteris***.

(*g*) T. S. leaf of ***Tmesipteris***.

22. Is the so called rhizome of ***Psilotum*** a gametophyte or sporophyte? Explain.

23. Describe the structure of sporangium in ***Psilotum***.

24. Compare the stem anatomy of ***Psilotum*** with that of ***Equisetum***.

25. Why is the sporangium of ***Psilotum*** called synangium?

26. Mention two features of gametophyte (prothallus) of ***Psilotum***,

27. Draw T. S. of synangium of ***Psilotum***, label the parts and describe its structure.

28. Give in brief the structure of gametophyte in ***Psilotum***.

29. Describe the distribution and structure of aerial branch of ***Psilotum***.

30. Give an account of the stele of the aerial shoot of ***Psilotum***.

31. Write about morphological nature of spore producing organs of ***Psilotum***.

(Himachal Pradesh, 2000)

32. Give an account of the state of the aerial shoot of ***Tmesipteris***.

33. Compare the synangia of ***Psilotum*** and ***Tmesipteris***.

34. Differentiate between ***Tmesipteris*** and ***Psilotum***.

35. How many species of ***Tmesipteris*** are known? Name at least two species.

36. What is the morphological nature of sporangial stalk in ***Tmesipteris***?

37. Describe, briefly, the external morphology of ***Tmesipteris*** sporophyte.

38. Name the spore bearing organ of ***Psilotum***.

(Kuvempu Univ., 2005)

39. Describe synangium of ***Psilotum***.

(Mysore Univ., 2004)

40. Discuss the development of antheridium and archegonium of ***Psilotum***.

(M.S. Univ., Tirun, 2005)

OBJECTIVE TYPE

38. Select the correct answer :

(*i*) ***Psilotum*** consists of

(*a*) Root and stem
(*b*) Root and leaves
(*c*) Stem and leaves
(*d*) Root, Stem and leaves.

(*ii*) Apical growth in ***Psilotum*** takes place by

(*a*) Apical cell
(*b*) Middle cell
(*c*) Basal cell
(*d*) Lateral cell.

(*iii*) The common characters shared by ***Rhynia*** and ***Psilotum*** are:

(*a*) Scale leaves
(*b*) Photosynthetic stem
(*c*) Rhizoids
(*d*) Sporangia.

(*iv*) Spore producing organ in ***Psilotum*** is known as

(*a*) Strobilus
(*b*) Sporangium
(*c*) Synangium
(*d*) Sorus.

(*v*) ***Psilotum*** belongs to the order

(*a*) Psilophytales
(*b*) Psilotales
(*c*) Lycopodiales
(*d*) Equisetales.

(*vi*) Three chambered sporangium is present in

(*a*) ***Lycopodium***
(*b*) ***Selaginella***
(*c*) ***Psilotum***
(*d*) ***Equisetum***.

(*vii*) An Angle leaf is present in the genus

(*a*) ***Psilotum***
(*b*) ***Lycopodium***
(*c*) ***Selaginella***
(*d*) ***Equisetum***.

(*viii*) In the rhizome of ***Psilotum***, the stele is
- (*a*) Solid protostele with central core of xylem surrounded byphloem
- (*b*) Mixed protostele
- (*c*) Actinostele
- (*d*) Dictyostele.

(*ix*) In ***Psilotum*** actinostele is present in the
- (*a*) Rhizome
- (*b*) Basal portion of the stem
- (*c*) Middle portion of the stele
- (*d*) Apical region of the aerial shoot.

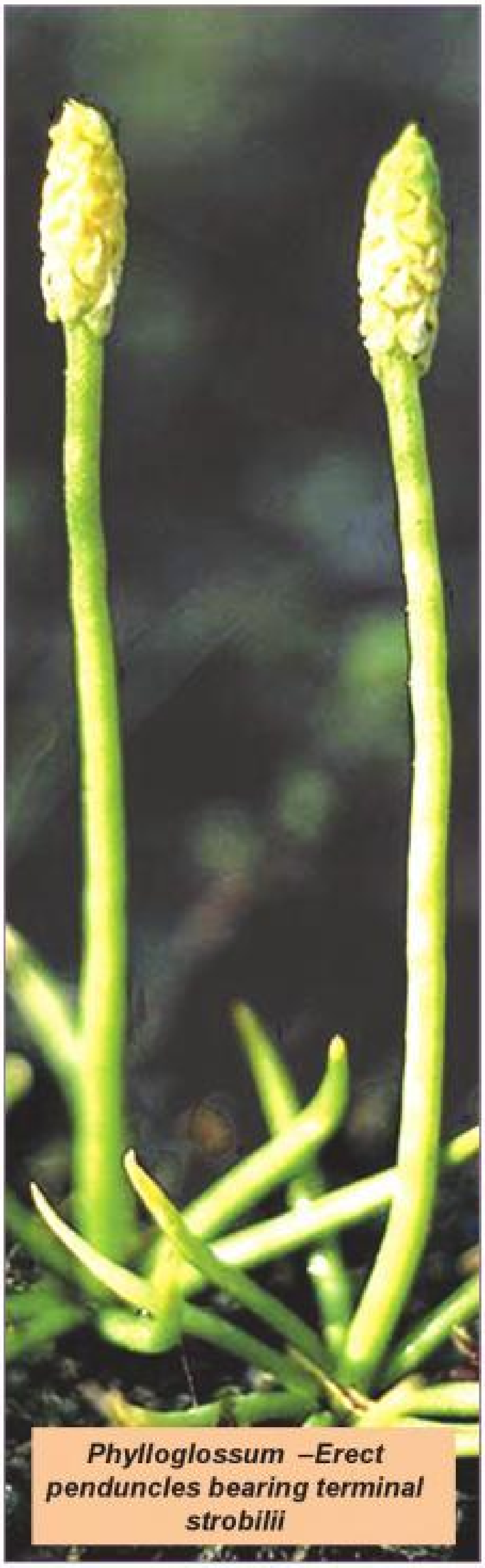
(*x*) In which of the following genus, the prothallus has well defined scalariforim reticulate tracheids surrounded by phloem and endodermis?
- (*a*) ***Psilotum***
- (*b*) ***Lycopodium***
- (*c*) ***Selaginella***
- (*d*) ***Equisetum.***

(*xi*) In which of the following roots are absent?
- (*a*) ***Lycopodium***
- (*b*) ***Selaginella***
- (*c*) ***Tmesipteris***
- (*d*) ***Equisetum.***

(*xii*) ***Psilotum*** differs from ***Tmesipteris*** in the
- (*a*) The structure of sex organs
- (*b*) Prothallus
- (*c*) The presence of rhizoids in both
- (*d*) The structure of synangium.

(*xiii*) The synangium in ***Tmesipteris*** is
- (*a*) One lobed
- (*b*) Two lobed
- (*c*) Three lobed
- (*d*) Four lobed

(*xiv*) The presence of a fungus is essential for the development of prothallus in
- (*a*) ***Psilotum***
- (*b*) ***Tmesipteris***
- (*c*) ***Lycopodium***
- (*d*) ***Selaginella.***


Phylloglossum –Erect penduncles bearing terminal strobilii

CHAPTER 4

Lycophyta–Eligulopsida

- Introduction
- Characteristic features
- Classification of Lycophyta
- Description of ***Lycopodium*** Linn
- ***Lycopodium selago*** and ***L. phlegmaria***
- ***L. clavatum*** and ***L. annotinum***
- ***L. cernuum*** and ***L. inundatum***

Introduction

The division Lycophyta is represented both by living and extinct genera and has a very long evolutionary history as it extends from the palaeozoic era to the present day. The living members of this sub-division are represented by five genera and 900 species that are widely distributed over the surface of the globe and occur under varied climatic conditions. The five living genera are :—

(1) *Lycopodium*,
(2) *Phylloglossum*,

(3) *Selaginella*,
(4) *Stylites* and
(5) *Isoetes*.

Selaginella

Characteristic features

1. Sporophytic plant body consists of roots, stems and spirally arranged microphyllous leaves.
2. Stems protostelic rarely polystelic.
3. May be homosporous or heterosporous.
4. Sporangia thick walled, usually develop on sporophyte.
5. Antherozoids biflagellate or multiflagellate.

Classification

Lycopodium

The division Lycophyta has been divided into two classes:

1. Class **Eligulopsida** which includes only one order :

(*a*) **Order Lycopodiales :** It comprises two families and has both living and extinct plants.

Family : **Lycopodiaceae.** It includes living as well as extinct plants ; herbaceous, cambium absent, sporophyll with sporangia arranged in loose strobili ; homosporous ; exosporic gametophytes; sperms biflagellate. The family includes ***Lycopodium***, ***Phylloglossum*** and ***Lycopodites*** (extinct).

2. Class **Ligulopsida**. It includes the following four orders :—

(*b*) Order **Selaginellales :** It includes both living and extinct forms. It is characterised by microphyllous and ligulate leaves which may be isophyllous or anisophyllous; strobili loose; heterosporous; gametophytes endosporic; secondary growth absent; spermatozoids biflagellate. It includes family **Selaginellaceae**.

(*c*) Order **Lepidodendrales :** Includes only extinct plants that had tree-like habit and possessed vascular cambium, microphyllous and ligulate leaves, distinct strobili and two types of spores (heterosporous). Some of the genera included in the family Lepidodendraceae are : ***Lepidodendron***, ***Stigmaria***, ***Sigillaria***, ***Lepidocarpon.***

(*d*) Order **Isoetales :** Includes both living and extinct forms. They are characterised by sporophytes with a cormlike stem; perennial root producing meristem; secondary growth; small and ligulate leave; two types of spores; endosporic gametophytes; and multiflagellate spermatozoids. It includes the family **Isoetaceae**.

(*e*) Order **Pleuromeiales :** It is an extinct order with tree-like sporophytes that bore ligulate microphylls near their apices. They were heterosporus. It includes family **Pleuromeiaceae** with **Peluromeia** as one of the genera.

The order **Lycopodiales** is characterised by herbaceous and dichotomously branched stems, microphyllous leaves, absence of secondary growth, sporangia axillary or on adaxial side of the leaf, homosporous, exosporic gametophytes, biflagellate sperms, protostelic or siphonostelic (***Phylloglossum***) stele; exarch or mesarch (***Phylloglossum***) xylem. The order includes the family ***Lycopodiaceae*** that includes two living genera, ***Lycopodium*** and ***Phylloglossum***. The life histories of ***Lycopodium*** and ***Phylloglossum*** are discussed in this chapter.

LYCOPODIUM Linn.

Distribution and Occurrence

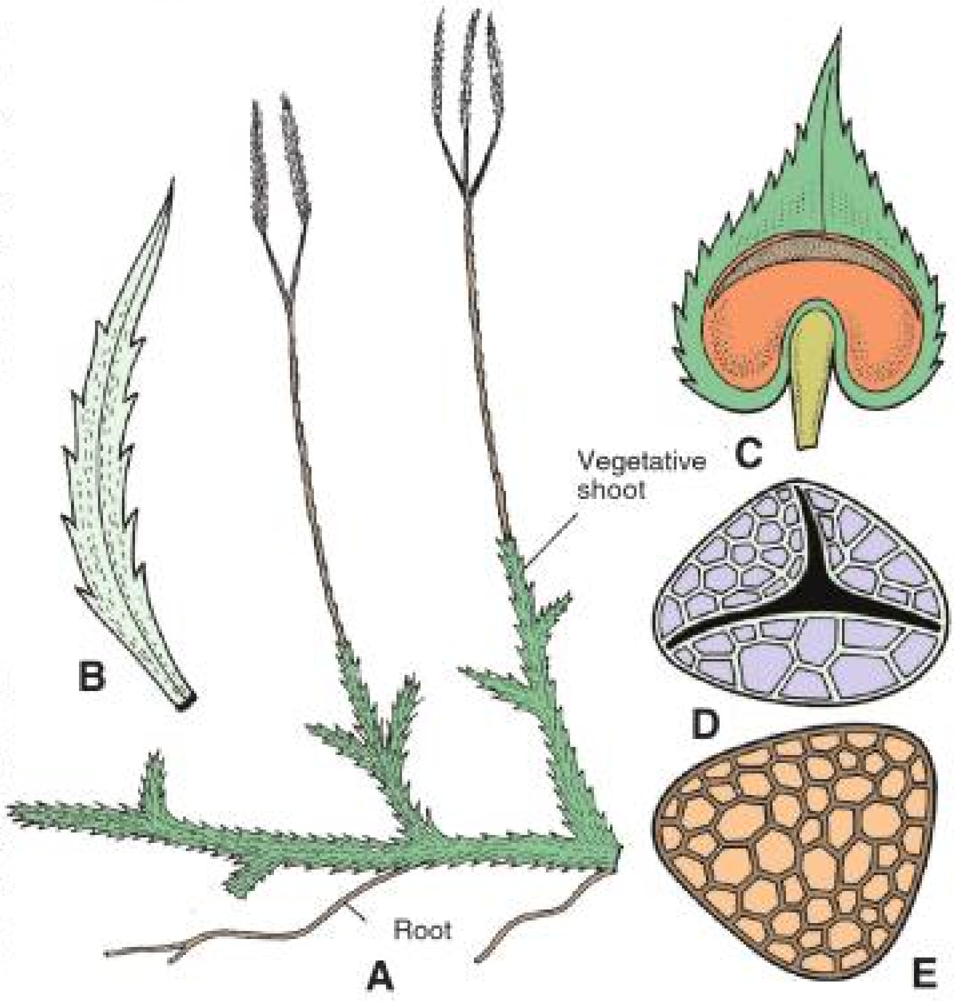
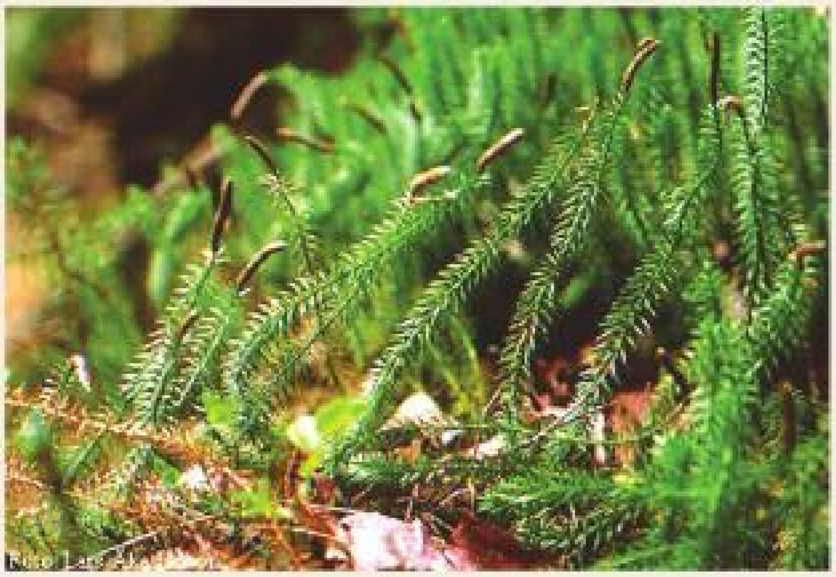


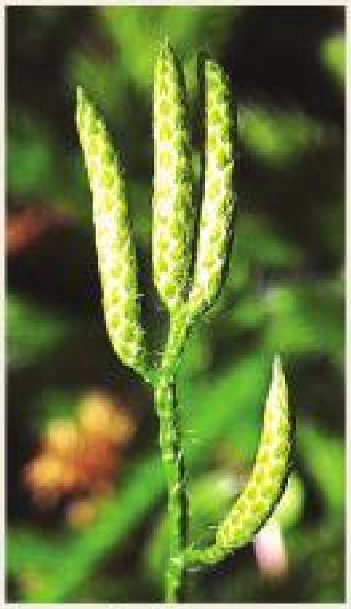
Fig. 4.1 (A–E). *Lycopodium clavatum*. **A.** Portion of a plant showing habit; **B.** A sterile leaf; **C.** A sporophyll bearing sporangium; **D.** A spore seen from above showing triradiate ridge; **E.** Spore showing reticulations of exine.

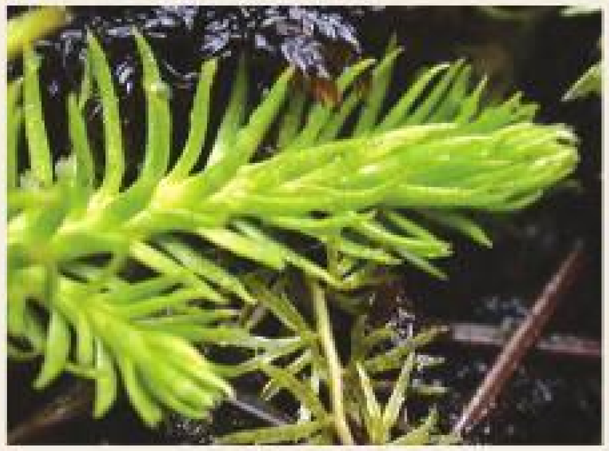
Lycopodium is a cosmopolitan genus with about four hundred species that are found under varied habitats. Some of them grow in the colder climates of the arctic region. There are others that inhabit temperate, tropical and sub-tropical regions of the world. They are very common in the tropical zones. In India the genus is represented by thirty-three species (Chowdhry, 1930, Panigrahi, 1962). Most of the species grow in Eastern Himalayas and in South Indian mountains. Mehra and Bir (1964) recorded twelve species from Darjeeling and Sikkim Himalayas. Bir and Vasudeva (1973) collected ***L. cernuum*** from Pachmarhi. Clarke (1880) reported two species from the western and eleven species from the eastern parts of the Himalayas. As many as nine species are found in Kodaikanal (South India), namely ***L. wightiana***, ***L. setaceum***, ***L. hamiltoni***, ***L. cernuum***, ***L. clavatum***, ***L. phlegmaria***, ***L. serratum***, ***L. complanatum and L. phyllanthum***. The stem is copiously covered with sharp and pointed leaves. Their moss-like appearance and club-shaped strobili, earn them the name 'club mosses'.

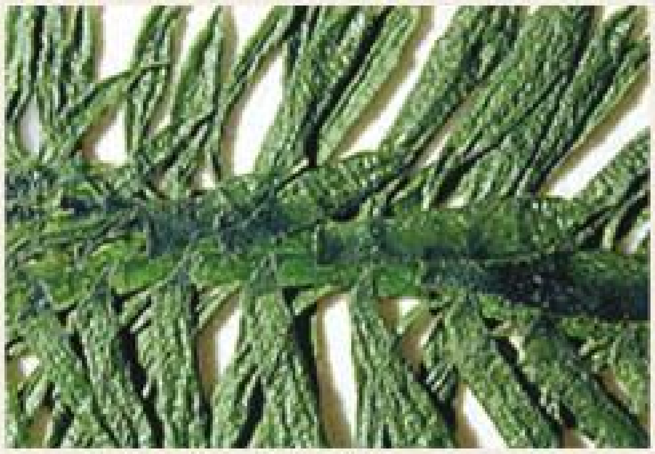
Habit

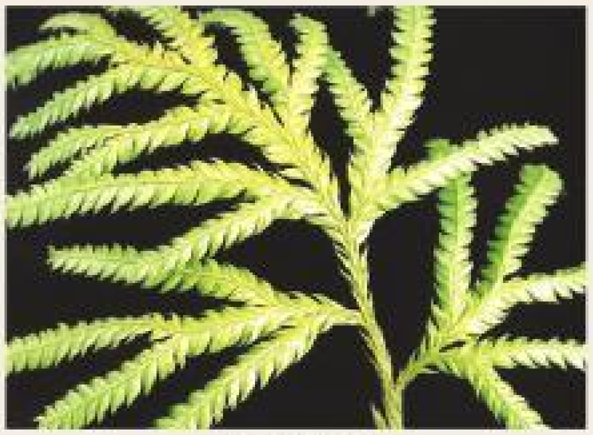
Most of the tropical species are epiphytic and grow hanging from the tree trunks e.g., ***L. phlegmaria*** (Fig. 4.3), ***L. squarrosum***, ***L. linifolium*** and ***L. funiform*** (all Indian species). ***L. phlegmarioides*** and ***L. carinatum*** are also epiphytic. The temperate species grow in open wood-lands and on moist and acidic soils. ***L. lucidulum*** and ***L. reflexum*** are erect and shrubby forms. ***L. annotinum*** is also an erect and terrestrial form. It is sparsely branched and not bushy. ***L. clavatum***, ***L. inundatum*** (Fig. 4.1, 4.4) and ***L. cernuum*** are common creeping forms. ***L. drumondii*** and ***L. carolianum*** have short creeping stems with erect strobilus bearing branches. ***L. volubile*** (Fig. 4.2) is a climber. The creeping forms give out erect branches at intervals. The erect and shrubby forms also have a creeping stem or the so called rhizomes which may be above ground in ***L. densum*** and subterranean in ***L. obscurum***. The erect branches in these species are much branched and appear bushy.

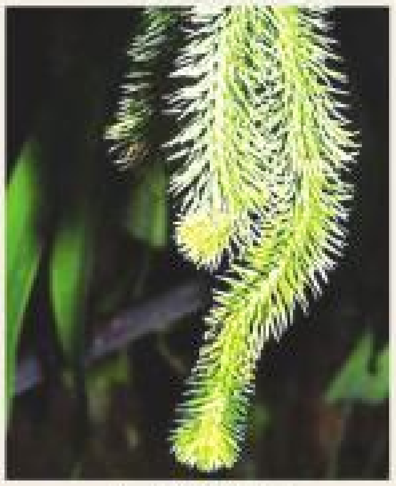

L. annotinum


L. clavatum


L. inundatum


L. lucidulum


L. volubile


L. squarrosum

Stem

The stem is dichotomously branched. The two branches formed as a result of dichotomy may be equal and continue to grow and undergo further dichotomy, or the two branches of a dichotomy may be unequal, ***i.e.***, one of them remains small and the other grows to a greater length. The smaller or the weaker branches may ultimately stop growth and bear strobili (Fig. 4.1). This type of branching (unequal dichotomy) is called **pseudomonopodial** (***L. clavatum***, ***L. densum***, ***L. obscurum***). In prostrate species the main axis or the rhizome is completely or partially subterranean.

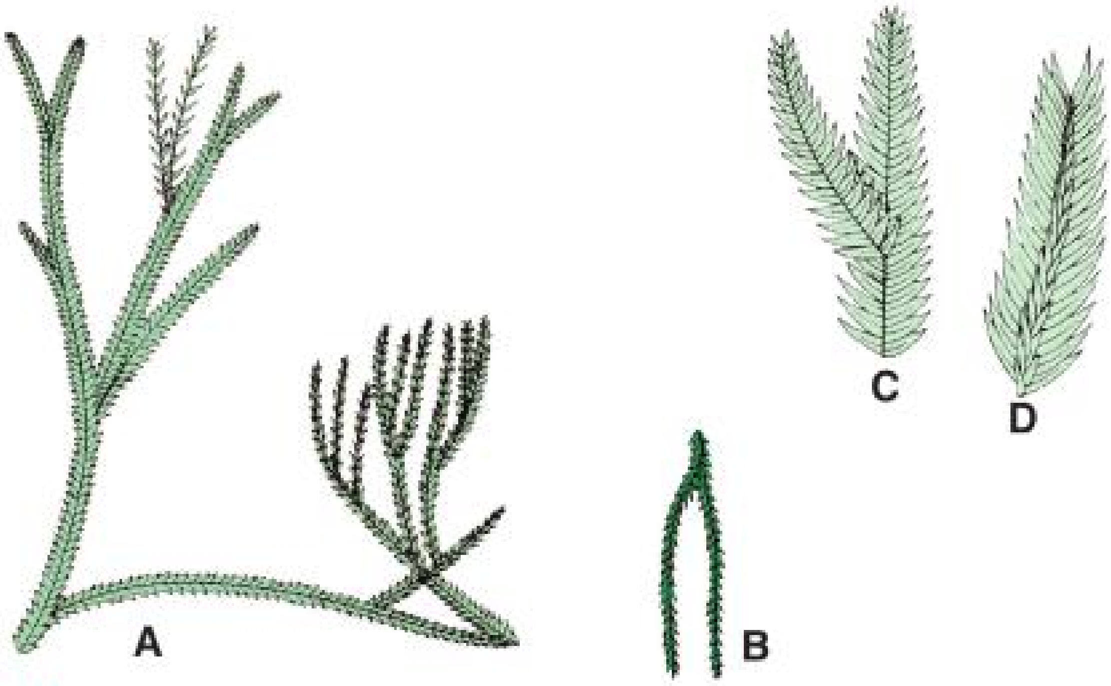
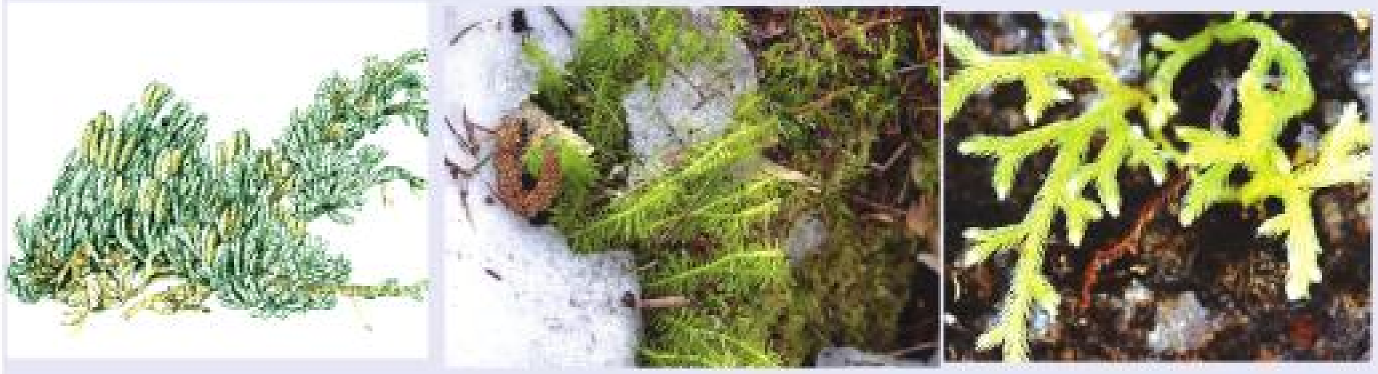


Fig. 4.2 (A-D). ***Lycopodium volubile***. **A.** Portion of a plant; **B.** Fertile branch with two strobili; **C.** Sterile branch with larger leaves in two lateral rows; **D.** Portion of branch with two lateral rows of large leaves and two rows of small leaves.

Leaf

The leaves are simple, sessile and small in size and possess a single median vein that fails to reach the leaf apex. Such leaves are called **microphyllous** or **microphylls**. The leaves are scale like in ***L. densum***. The leaf margin may be entire or serrate (***L. serratum***). The leaf base is decurrent in ***L. complanatum***. The leaves lack a ligule. Usually the leaves are 2—10 mm. long but in some cases their length reaches 2 to 3 cm. long. The leaves are spirally arranged and densely cover the branches. In some cases the leaf arrangement may be decussate (***L. alpinum***) or even whorled (***L. verticillatum***, ***L. nikoense*** and ***L. cernuum***). The phyllotaxis appears to be opposite in the mature plant of ***L. complanatum*** (Bhambie, 1965).



L. alpinum *L. serratum* *L. cernuum*

The leaves may be **isophyllous** or **anisophyllous** (***L. volubile***). The branches in ***L. volubile*** bear four rows of leaves : two lateral rows of large and falcate leaves, ventral row of small hair-like leaves, and a dorsal row of medium sized acicular leaves. The creeping axis bears long and needle-like leaves. In addition to the normal leaves the bulbils in ***L. selago*** develop thick and fleshy leaves. In ***L. clavatum*** the strobilus bearing or fertile branches bear scale-like vegetative leaves that are yellowish green in colour. The sterile branches bear large linear and green leaves that are dentate.

Root

The roots are dichotomously branched, adventitious and arise endogenously from the lower side of the prostrate stems in an acropetalous manner. The ephemeral primary root of the young sporophyte soon dies.

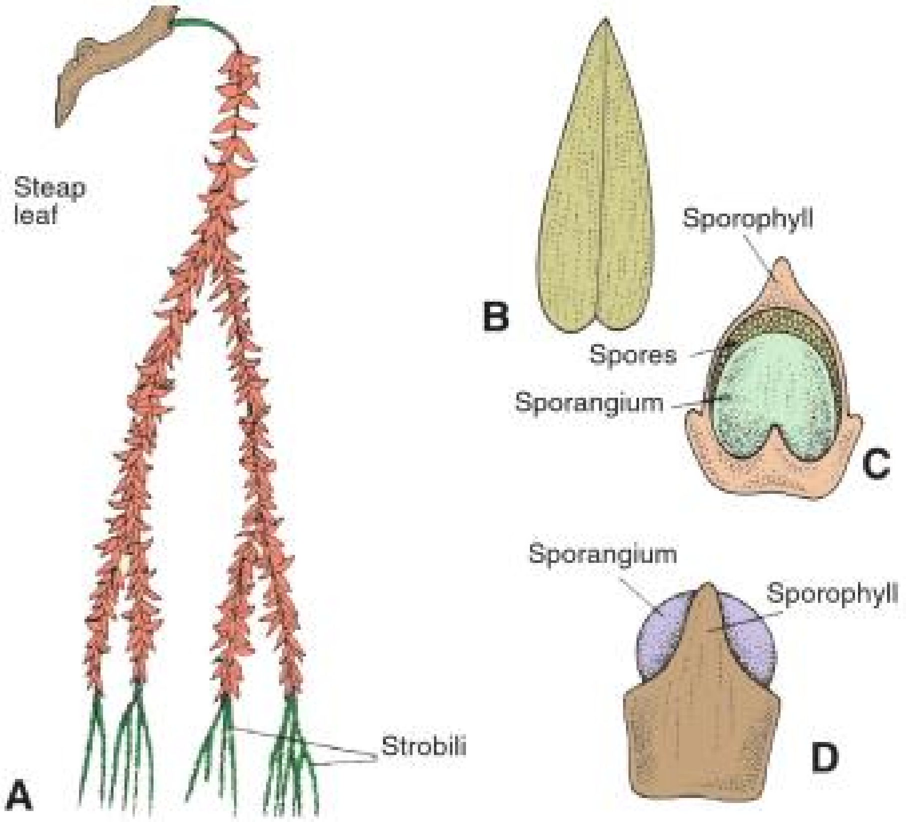
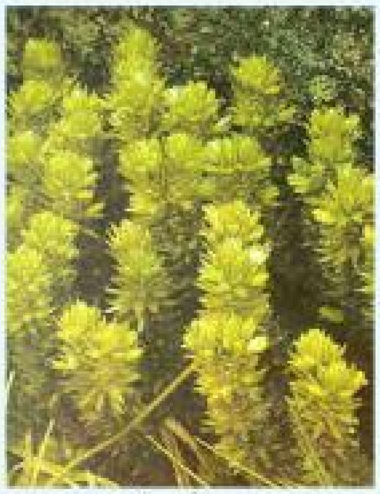


Fig. 4.3 (A–D). *Lycopodium phlegmaria.* **A.** The plant hanging from the host tree and showing pendent branches and strobili; **B.** A leaf ; **C-D.** Sporangia with sporophylls.

In the erect forms the roots come out from the basal part of the stem. There are no roots elsewhere along the entire legnth of the stem. In such cases the adventitious roots initiate near the shoot apex but do not come out of the stem, instead they grow downwards through the cortex and emerge out of the stem only near its base. A series of transverse sections of such stems shows numerous roots in the cortex (Fig. 4.12). Such roots are called **cortical roots** and are found in ***L. selago***, ***L. pithyoides***, ***etc***. Stockey (1907) reported as many as 52 cortical roots at one level of stem in ***L. pithyoides***. This is due to their acropetalous origin. The roots on coming out of the stem (aerial roots) branch freely in a dichotomous manner. In ***L. clavatum*** and ***L. cernuum*** (prostrate forms) the creeping axis bears adventitious roots all along its length. In these cases the root primordia take more direct course through the cortex.

Rothmaler (1944) suggested, on account of the variations in the genus, to split it up into four genera. He named these genera as ***Lycopodium***, ***Lepidotis***, ***Diphasium***, and ***Huperzia.*** Rothmaler's treatment is also supported by the recent cytological investigations of the various species. His four genera show a complete cytological disparity. Pritzel (1900) divided the genus into two sub-genera which he named as ***Rhopalostachya*** and ***Urostachya***. The former includes all those species that have prostrate main stems giving out erect secondary branches (***L. clavatum*** and ***L. cernuum***). The latter includes the erect and epiphytic species (***L. pithyoides***, ***L. selago***, ***L. selago***, ***L. phlegmaria***, etc.).



L. selago

L. phlegmaria

The **Urostachya** are regarded as primitive and show the following characters :— (*i*) they have erect or pendulous aerial axis; (*ii*) the adventitious roots emerge out at the base; (*iii*) vegetative propagation by bulbils is common; (*iv*) lack of specialisation of the sporophylls.

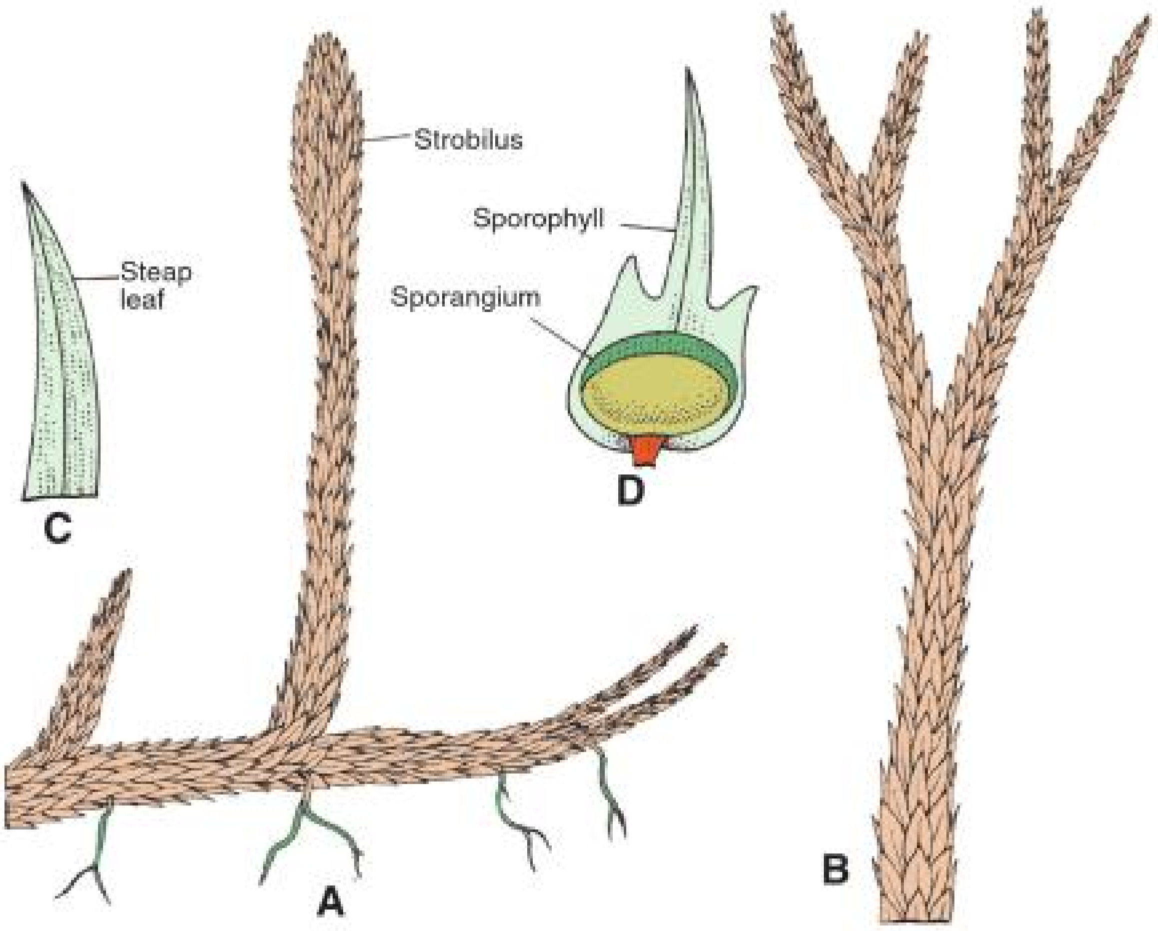
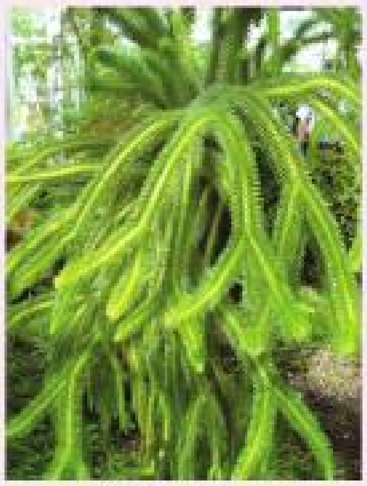


Fig. 4.4. *Lycopodium.* External morphology. **A.** *L. inundatum*; **B.** *L. selago* ; note that the sporangia occur scattered and do not form a distinct strobilus; **C.** A sterile leaf from A; **D.** A sporophyll with sporangium from A.



Huperzia

Diphazium

The Rhopalostachya show the following features:— (*i*) the main stem prostrate; (*ii*) bulbils rare; (*iii*) sporophylls specialised; (*iv*) the roots may emerge at any point so that the whole axis is covered by adventitious roots.

Love ***et. al.***, (1977) classified the genus on cytological grounds into two families ***i.e.***, the **Huperziaceae** and **Lycopodiaceae**. In the former he included the genera ***Huperzia*** and ***Phlegmariurus***, whereas in the latter he included the genera ***Lycopodium***, ***Diphazium***, ***Diphasiastrum***, ***Palhinhaea***, ***Lepidotis***, ***Lycopodiella***, ***Diphasiopsis***, ***Pseudolycopodium***, ***Lycopodiastrum*** and ***Lateristachys***. Pichi-sermolli (1977) recognised only family ***Lycopodiaceae*** and included six genera in it.

Growth

The growth of the shoot takes place by means of an apical meristem which consists of a group of apical cells (Fig. 4.5). The derivatives of these cells differentiate into the primary meristematic tissue : the **protoderm**, the **ground meristem** and the **procambium**. The protoderm gives rise to the outer protective layer of the epidermis. The ground meristem differentiates the cortex, endodermis, pericycle and the pith. The procambium gives rise to the vascular tissue (xylem and the phloem). Wetmore (1943) has shown that the procambium is centrally located and extends very close to the shoot apex. Its cells are enlongated and usually divide in a longitudinal plane and only frequently in transverse plane.

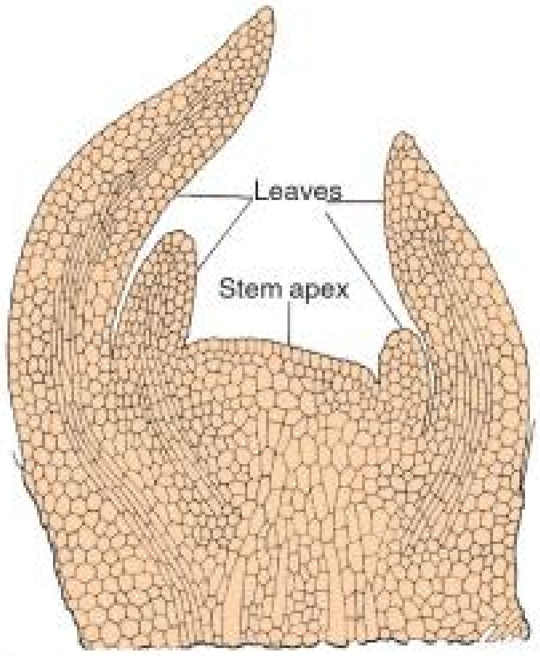


Fig. 4.5. Longitudinal section of stem-apex of *Lycopodium reflexum.*

ANATOMY

Stem

A transverse section of the stem reveals :

Epidermis

It is a single layer of parenchymatous cells with cutinised outer walls and stomata.

Cortex

It is present next to the epidermis and shows a great variation in its thickness and structure. Usually three types are recognisable :—

1. In some cases the whole of the cortex is made up of thin-walled cells. They enclose small or larger intercellular spaces. Such a cortex is called homogenous (***L. selago***).
2. In some species the cortex in the mature stems is made up wholly of sclerenchymatous cells. There are no intercellular spaces between the cells.
3. In others (***L. clavatum***) the cortex is differentiated into three zones (Fig. 4.6, A).
    - (*i*) The outer zone of thick-walled cells (**Hypodermis**)
    - (*ii*) The middle zone of large and thin-walled cells. These cells enclose lot of intercellular spaces.
    - (*iii*) The inner zone of thick-walled cells.

In ***L. cernuum*** the outer and inner cortex are thin-walled and the middle cortex is sclerenchymatous (Fig. 4.6, B).

The stem diameter and its position also effect the composition of the cortex. In the underground stems the cortex is usually entirely sclerenchymatous. In stems with smaller diameter the cortex may be entirely parenchymatous or chlorenchymatous and the cells are usually loosely arranged. The sclerenchyma is either absent or greatly reduced. The above ground stems with larger diameter usually show differentiation into chlorenchymatous, parenchymatous and sclerenchymatous cortex.

The last layer of cortical cells is called the **endodermis**. Endodermis is clearly recognisable in the earlier stages of development because of the presence of casparian strips. As the development proceeds, in mature stems, the endodermal cells become thickened.

Pericycle

It is present next to the endodermis and is composed of one or many layers of compactly arranged parenchymatous cells.

Vascular Region or the Stele

It consists of only primary tissue ***i.e.***, the primary xylem and the primary phloem. The sporelings of all the species of ***Lycopodium*** show a central protostele with radiating arms, ***i.e.***, **actinostelic** condition. When the sporelings grow the stelar structure goes on becoming complex and shows variations in various species. Sometimes the arrangement differs at different levels in the shoot of same species. Basically the arrangement of primary xylem and phloem is a **protostele**. In this case the xylem forms the central core of the stem and pith is absent. The phloem surrounds the xylem (Fig. 4.6, C). The protostele, as studied in the various species of ***Lycopodium*** shows variations with respect to its shape and arrangement of vascular tissue (xylem and phloem). It may be :—

(***i***) **actinostele** (Fig. 4.6, C) in which the xylem appears star-shaped with protoxylem situated at the (Fig. 4.6, C) tips of the star-shaped projections and is exarch (*L.* ***selago***, *L.* ***serratum.*** *L.* ***phlegmaria***) ; (***ii***) **plectostele** in which the xylem, in a transverse section, appears to be in form of separate plates of (*L.* ***volubile***, *L.* ***clavatum***) variable sizes with phloem in between them (Fig. 4.6, A); and (***iii***) **mixed protostele** in which the xylem and phloem are uniformly distributed and in a transverse section, it appears as if strands of xylem are embedded in the phloem (Fig. 4.6, B) which forms the ground mass (*L.* ***cernuum***). The xylem is exarch.

In a plectostele the separate bands of xylem and phloem appear interconnected in a longitudinal section. They remain free only up to a certain distance up and below. In a mixed protostele the xylem occurs in the form of irregular tracheids scattered in the ground mass of phloem (Ogura, 1938). It is also found in ***L. lateralis*** and ***L. drummondii.***

L. lateralis

There is no doubt that the arrangement of vascular elements varies with species but on the other hand it has also been observed (Wardlaw, 1924, Bierhorst, 1971) that the diameter of the stem also plays a significant role in effecting this variation. In some species the stems with smaller diameter have actinostelic protostele whereas in the same species the stems with larger diameter have plectostelic protostele ***e.g.***, *L.* ***densum***. In *L.* ***phlegmarioides*** the stele may be plectostelic in some parts and a mixed protostele in parts with larger diameter.

The protoxylem elements are composed of annular or spiral trachieds. Sometimes the rings in the annular tracheids are inter-connected with each other by one or two oblique or vertical bands of thickening. Bierhorst (1960) has reported the tracheids of the metaxylem to have circular bordered pits (*L.* ***selago***, *L.* ***serratum*** and ***L. lucidulum***) or sometimes sclariform pits. The end walls of the tracheids are oblique and possess elongated pits. The phloem is composed of sieve cells and phloem parenchyma. The sieve cells are long and tubular with sieve areas on the lateral as well as end walls. The sieve elements develop centripetally from outer angles towards the centre. The vessels are absent.

Strands of vascular tissue called the **leaf traces** extend outwards from the stele and run obliquely upwards through the cortex. Only one strand enters the leaf to form a single median vein. Similarly stele is connected with each branch by a **branch trace**. In a transverse section the leaf traces appear as distinct vascular strands.

There are no leaf gaps.

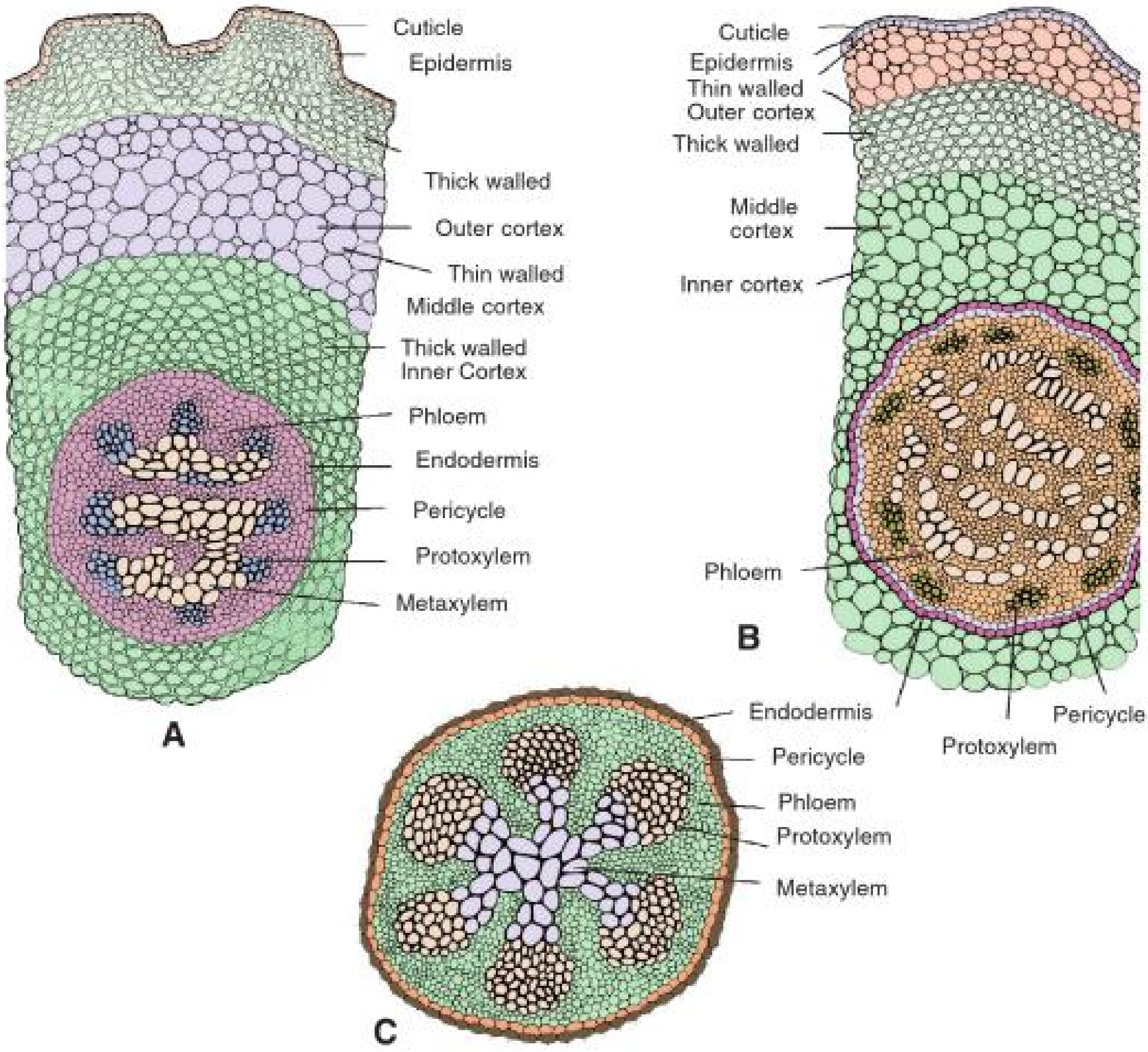

Cuticle
Epidermis
Thick walled
Outer cortex
Thin walled
Middle cortex
Thick walled
Inner Cortex
Phloem
Endodermis
Pericycle
Protoxylem
Metaxylem
A
Cuticle
Epidermis
Thin walled
Outer cortex
Thick walled
Middle
cortex
Inner cortex
Phloem
B
Endodermis
Pericycle
Protoxylem
Pericycle
Phloem
Protoxylem
Metaxylem
C

Fig. 4.6. ***Lycopodium***–Stem anatomy. ***A. L. clavatum.*** T.S. portion of stem. Note inner sclarenchymatous cortex and plectostelic-protostele; ***B. L. cernuum.*** The middle cortex is sclerenchymatous. The stele is a mixed protostele; ***C. L. serratum.*** Actinostelic protostele

Leaf

In ***Lycopodium clavatum*** the leaf has s triangular outline in a transverse section. In ***L. selago*** (Fig. 4.7) the leaf is almost flattened. A transverse section reveals the following structure :—

Epidermis

The epidermis is a single layer of compactly arranged cells with sinuate and thick outer periclinal walls which are also covered by a layer of cuticle. It is perforated by stomata. The cuticle extends over the guard cells. The stomata may be on both the sides of the leaf in isophyllous species and only on lower epidermis in some anisophyllous species (***L. volubile***, ***L. complanatum***).

Mesophyll

It is undifferentiated and consists of loosely arranged chlorophyllose cells with small or large intercellular spaces. The cells may be round or oval or slightly lobed.

Vascular Region

A single unbranched vascular strand traverses the leaf. The vascular bundle is **mesarch.**

The xylem does not always show a clear distinction into proto and metaxylem. Protoxylem when distinct is surrounded by metaxylem. Phloem is conspicious only in the basal region of the leaf and surrounds the xylem. Near the apex of the leaf, vascular strand is composed by xylem alone. The tracheids in the xylem have spiral or annular thickenings. The phloem consists of sieve tubes and phloem parenchyma. The sieve tubes have narrow lumen. Endodermis or the bundle sheath may or may not be distinct.

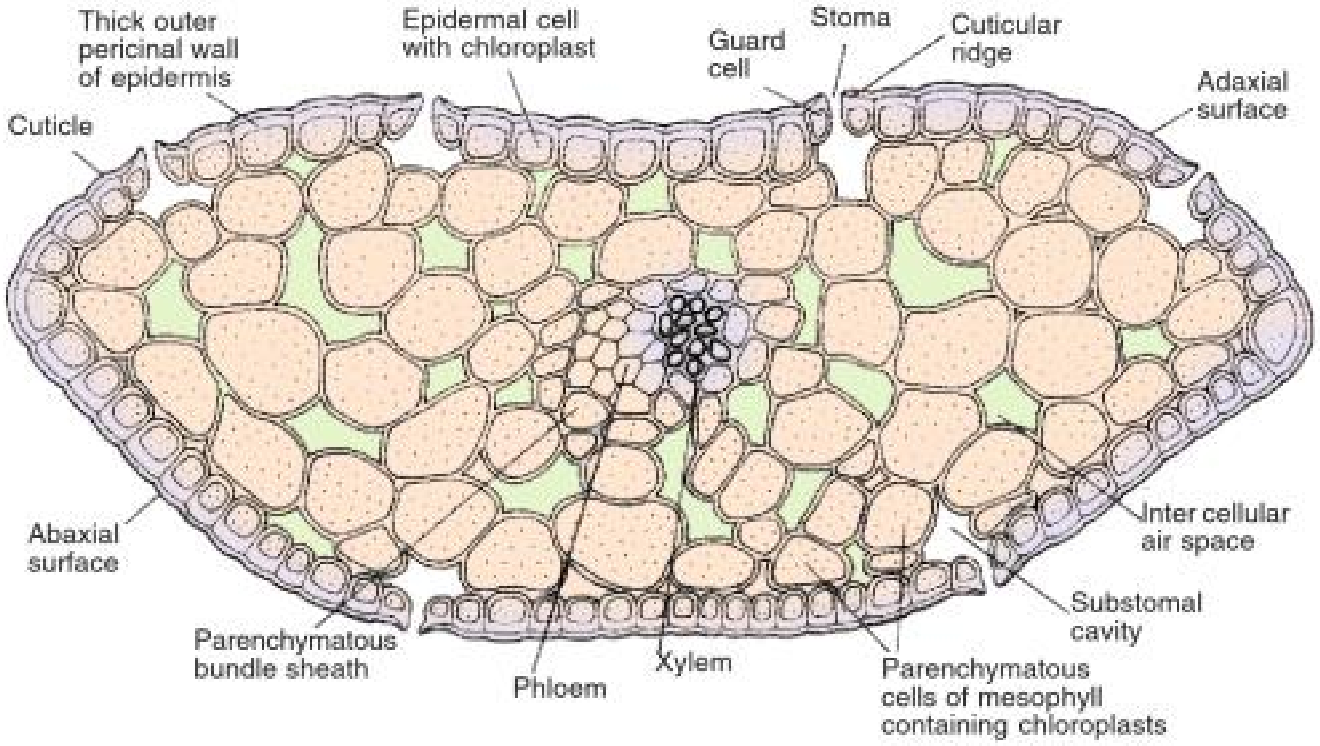

Thick outer pericinal wall of epidermis
Epidermal cell with chloroplast
Guard cell
Stoma
Cuticular ridge
Adaxial surface
Cuticle
Abaxial surface
Inter cellular air space
Substomal cavity
Parenchymatous bundle sheath
Phloem
Xylem
Parenchymatous cells of mesophyll containing chloroplasts

Fig. 4.7. ***Lycopodium selago*****,** V.S. leaf.

Root (Fig. 4.8, A–C)

The adventitious roots arise from the pericycle. A transverse section of the aerial root reveals the following structure:

Epidermis (Fig. 4.8, A)

It consists of a single layer of thin-walled cells and is covered by numerous root hairs. The root hairs are arranged in pairs and their origin is characteristic for the genus ***Lycopodium***. An epidermal cell divides either by an anticlinal or by an oblique wall into two daughter cells. These are called the **root hair initials**. Both of them give out root hairs which therefore, lie in pairs. Epidermis is persistent in the aerial roots.

Cortex

In mature roots the cortex forms a broad zone and can be differentiated into two distinct regions. The outer cortex which is composed of several layers of thick-walled cells (Fig. 4.10) and the inner parenchymatous cortex. Endodermis and pericycle are not distinguishable.

Stele

The stele may be diarch, tetrarch, or polyarch. In most of the prostrate or creeping species ***e.g.***, ***L. clavatum***, the stele is polyarch. There is no pith and the stele consists of six to ten plates of xylem arranged in a radial fashion. The xylem is exarch. The metaxylem of each radial plate of xylem unites in the centre to give a star-shaped appearance. The phloem is present in the form of patches in between the radiating arms of xylem. This structure is just like the actinostelic prostostele.

In most of the erect and epiphytic species the stele is diarch or tetrarch. In ***L. pithyoides*** it is diarch and the xylem is crescent-shaped with protoxylem at the ends ***i.e***., exarch. The phloem occupies the region between the two ends of the crescent-shaped xylem ***i.e***., on the concave side. There is only one group of phloem.

In ***L. selago*** the stele is diarch in one part of the root and tetrarch in the other. The diarch condition (Fig. 4.8, A, B) is similar to the one described for ***L. pithyoides***. In tetrarch condition the stele reveals two separate bands of xylem with protoxylem at either end (exarch). The phloem lies between the xylem bands. This condition is somewhat similar to the plectostelic protostele. In some cases more than two groups of protoxylem occur on the convex sides. Sometimes the entire convex side is covered with protoxylem tracheids.

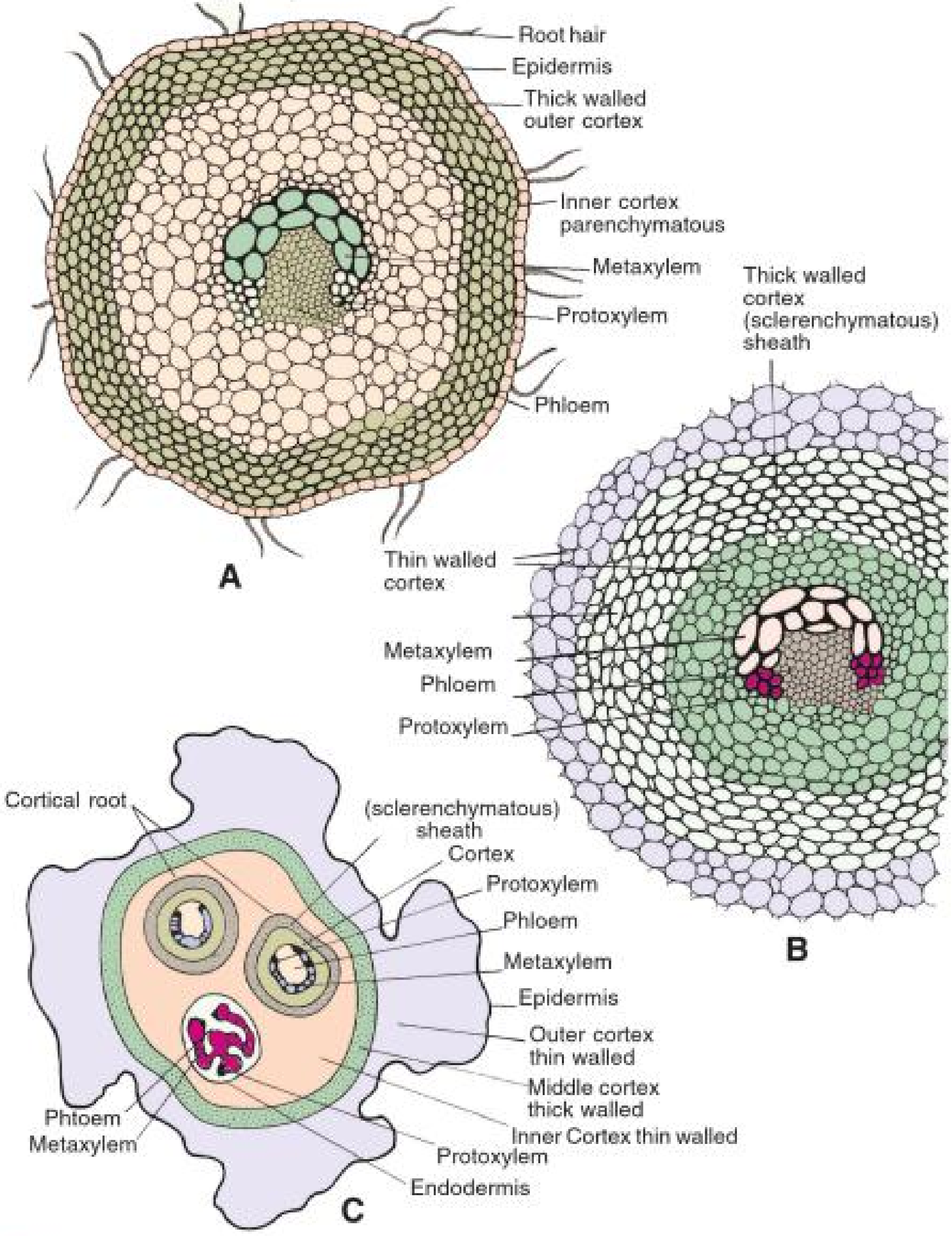

Root hair
Epidermis
Thick walled outer cortex
Inner cortex parenchymatous
Metaxylem
Protoxylem
Phloem
A
Thick walled cortex (sclerenchymatous) sheath
Thin walled cortex
Metaxylem
Phloem
Protoxylem
B
Cortical root
(sclerenchymatous) sheath
Cortex
Protoxylem
Phloem
Metaxylem
Epidermis
Outer cortex thin walled
Middle cortex thick walled
Inner Cortex thin walled
Protoxylem
Endodermis
Phtoem
Metaxylem
C

Fig. 4.8. ***Lycopodium selago.*** T.S. Root. **A.** T.S. Aerial Root; **B.** T.S. Cortical Root; **C.** Diagrammatic T.S. through stem showing one stele and two cortical roots.

The cortical roots (Fig. 4.8, B and C) are almost similar in their internal organisation to the aerial roots. In the cortical roots the epidermis is not persistent and the root hairs are absent or appear as small protuberances (trichoblasts). The cortex is usually wholly sclerenchymatous or may be partly so.

VEGETATIVE PROPAGATION

The sporophyte of ***Lycopodium*** reproduces vegetatively by the following methods :—

1. By the Formation of Gemmae or Bulbils (Fig. 4.9, A–C)

These are modified vegetative structures that arise as lateral out-growths from near the stem apices and take the place of leaves. They have been reported in ***L. selago***, ***L. phlegmaria*** and ***L. lucidulum***. Each bulbil consists of a short and reduced axis surrounded by a number of thick and fleshy leaves. These leaves store food material. They remain on the plant till root primordia appear on the shortened stem. The gemmae fall on the ground and grow into a young plant.

Morphology of the Bulbil

There has been a considerable discussion regarding the morphological nature of the bulbil. This has been regarded on purely morphological basis as being a modified sporangium, an arrested shank of a dichotomy, a lateral branch or a modified leaf. Its leaf-like nature is supported by the facts that bulbils stand in the place of leaves in the phyllotatic spiral and that their vascular supply is similar to the leaf trace in anatomical construction and in relation to the axial stele (Smith, 1930). Experiments on ***L. selago*** (S. Williams, 1933) show that if shoots of young plants are decapitated immediately below the apex, the young leaf rudiments transform into regenerative buds.

2. Fragmentation

Death and decay of older regions of the stem leading to the separation of younger branches which grow into separate plants is also a common method of vegetative propagation in ***Lycopodium.***

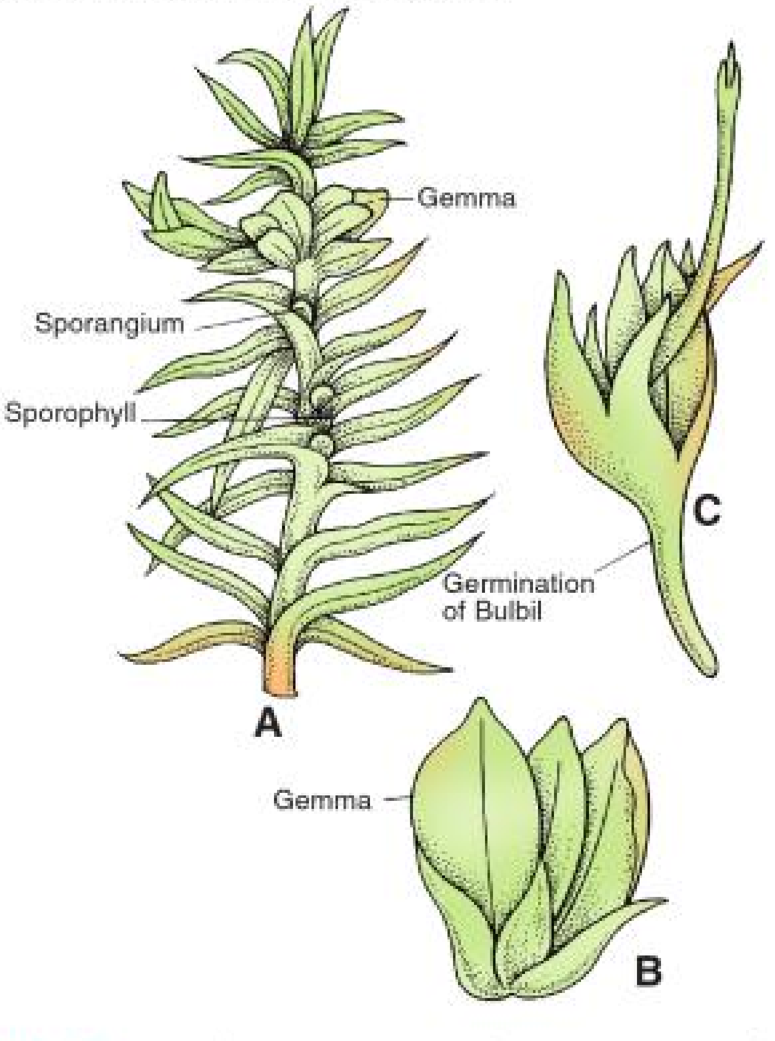


Fig. 4.9. *Lycopodium*. Vegetative reproduction. **A.** Portion of stem of *L. lucidulum* bearing gemmae; **B.** A gemma; **C.** Germinating gemma of *L. selago.*

3. Formation of Resting Buds

In ***L. inundatum***, the tips on the apical buds of rhizome and its branches store food material and become surrounded by densely crowded leaves. These are the resting buds. In winter the rest of the plant except these resting buds dies. At the advent of favourable conditions the resting buds resume growth and give rise to new plants.

4. Formation of Root Tubercles

In ***L. ramulosum*** (Holloway, 1917), tubercles originate from the parenchymatous region of the root cortex. They consist of a group of cells with stored food material and protected by thick walls and have the capacity to germinate into new plants.

5. Formation of Adventitious Buds

Such buds have been induced on isolated bulbil leaves. In the leaves epidermal cells proliferate near the base and grow into buds. Decapitation of stem near its apex also induces the formation of such buds. In this case the leaf rudiments change into such buds. Such experiments of adventitious bud induction were carried out on ***L. selago*** by Williams (1933). Goebel reported the formation of such buds from isolated leaves of sporelings in ***L. inundatum.*** These buds are capable of germinating into new plants.

ORGANISATION OF THE STROBILUS

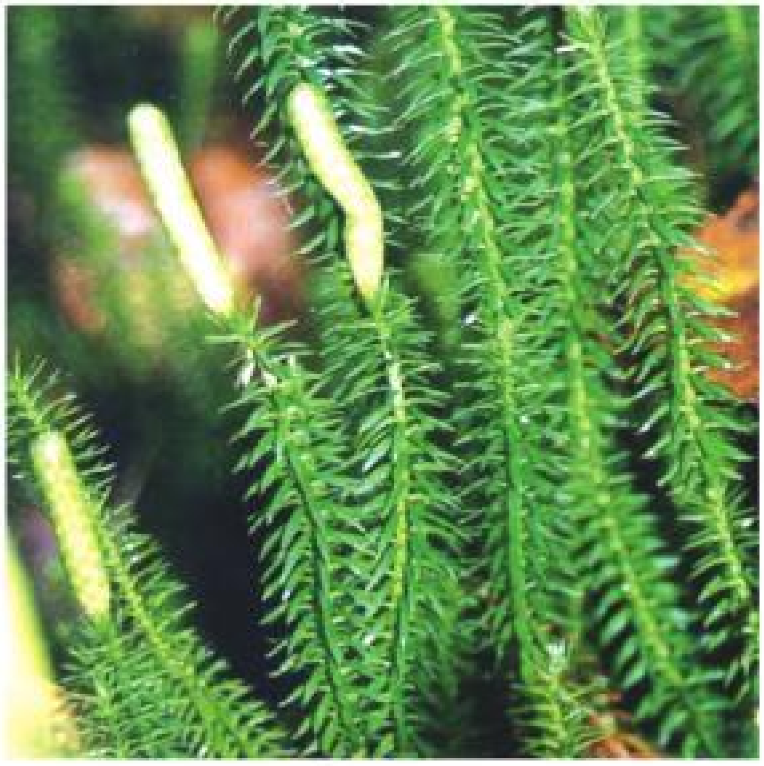
In the simple and primitive species of ***Lycopodium*** all of which belong to the ***Urostachya*** (***L. selago***, ***L. lucidulum***, ***L. squarrosum***, etc.) every leaf on the plant is a sporophyll or at least potentially so. In the species belonging to ***Rhopalostachya*** and in some species belonging to ***Urostachya*** (***L. phlegmaria***) the leaves near the apices of the branches bear sporangia and are called the **sporophylls**. The lower leaves in these species are sterile and function merely as foliage leaves. Aggregation of sporophylls is called the **strobilus**. The arrangement of the sporophylls may be loose when they form a lax or a loose **strobilus** or they may be arranged compactly to form a compact or a definite **strobilus**. The compact type of strobilus is a stem with short internodes bearing sporophylls. It develops from an apical meristem and its vasculature is similar to that of vegetative axis.

In ***L. selago*** and ***L. reflexum*** (Fig. 4.4, B) the sporophylls are similar to the foliage leaves and are arranged in a loose manner at intervals all along the erect branches. Such an arrangement gives rise to alternating fertile and sterile regions. Such a condition is regarded by many morphologists as a strobilus comprising the entire plant. The supporters of this view regard the foliage leaves as secondarily sterilised sporophylls. Such a conclusion is based on the observation that such leaves also bear abortive sporangia. The same is the condition in ***L. lucidulum***. In ***L. squarrosum*** the strobilus is terminal in position but can be hardly distinguished from the sterile region because the sporophylls are similar to the foliage leaves and are loosely arranged.

In ***L. phlegmaria*** (Fig. 4.3) the sporophylls are smaller than the foliage leaves and are arranged in a compact manner to form distinct strobili (Fig. 4.3) at the distal ends of the stem and its branches. The strobili in this species are dichotomously branched and pendulous.

In the section ***Rhopalostachya*** there is a great variatioin among the sterile leaves and the sporophylls. In ***Lycopodium inundatum*** (Fig. 4.4, A) the sporophylls differ only slightly from the sterile leaves and the strobilus is not very distinctly marked off from the vegetative shoot. The sporophylls are slightly modified (Fig. 4.4, D) so as to protect the sporangium.

In ***Lycopodium annotinum*** the strobilus is quite distinct from the vegetative shoot. The sporophylls are quite distinct from the sterile or vegetative leaves. Each sporophyll has an abaxial outgrowth or a flange that protects the sporangia belonging to the lower sporophylls. The strobili of this species terminate normal leafy branches and the sterile leaves are all alike.



Lycopodium annotinum

In ***L. clavatum*** (Fig. 4.1) the strobili are quite distinct and compact and are borne at the tips of special erect shoots. There is segregation of fertile and sterile branches. The sporophylls possess a small flange on ventral side. It protects the sporangium below (Fig. 4.10, D).

In ***L. volubile*** (Fig. 4.2, A–D), the strobili terminate younger branches and are compact and branched (Fig. 4.2, B). The sporophylls possess a small bulge or a flange on the ventral (abaxial) side. This outgrowth affords some protection to the sporangia below.

In some species with distinct strobili the strobilar apex, under special growth conditions, continues its growth to produce a vegetative extension of the strobilus ***e.g.***, ***L. obscurum*** and ***L. flabelliforme***. The same is the case in ***L. drummondii*** where the strobiler apex resumes growth at a later stage to produce a vegetative region which again bears a strobilus and this sequence is repeated many times.

There is a considerable variation regarding the position of the sporangium with respect to the sporophyll. In ***L. selago***, ***L. phlegmaria*** (Fig. 4.10, E) ***L. lucidulum*** and ***L. inundatum*** the sporangia are **axillary** in position. In ***L. cernuum*** and ***L. clavatum*** (Fig. 4.10, A and D) the sporangium arises on the dorsal (adaxial) surface of the sporophylls, that is, it is '**foliar**' or '**epiphyllous**'. In ***L. squarrosum*** the position is **sub-foliar**, that is, in this case the sporangium does not arise exactly on the sporophyll, but a little towards the sporophyll. Every sporophyll is supplied, from the stele of the stem by a single trace.

A careful perusal of the facts cited above reveals that in the simpler species where there is no or very little differentiation between vegetative and reproductive regions, the stems are dichotomously branched and possess a radial type of stele. The cone bearing species on the other hand have stem with pseudo-monopodial branching and most of them show the parallel-banded type of stele.

SPORANGIUM

The sporangium is mostly reniform or kidney-shaped (Fig. 4.1 C 4.2 C D; 4.10) and sometimes sub-spherical. It is usually raised on a short and massive stalk (Fig. 4.10). The stalk of the sporangium is indistinct in some species. The sporangia arise singly and may be exposed or protected. They are exposed in ***L. squarrosum***, ***L. lucidulum*** (Fig. 4.9, A), ***L. selago*** etc., and protected in ***L. inundatum***, ***L. cernuum***, ***L. clavatum etc***. In the latler case they are protected by flange-like outgrowth from the sporphylls above. They vary in colour from orange to yellow. The usual length of sporangium is two milimeters or a little more.

Structure of the Sporangium

The sporangium is clearly distinguishable into two (fig. 4.11, F, G) prominent parts : (***i***) the **stalk** and (***ii***) the **capsule**.

The stalk may be short and distinct as in ***L. phlegmaria*** (Fig. 4.10, E) or may be just represented by a cushion of cells (***L. cernuum***). It may be narrow as in ***L. selago*** or broad as in ***L. alpinum***.

The stalk bears a curved and reniform capsule which is not lobed and is unilocular (Fig. 4.10, A). It has a three or more layered wall surrounding a mass of spore mother cells (Fig. 4.11, G). In ***L. selago*** the sporangial wall is three layered at the apex and may be more than three layers near its base. The innermost layer of wall is called the **tapetum**. The tapetum forms a complete investment of the sporogenous tissue. Its cells are prominent due to the more granular nature of their cytoplasm and bigger nuclei. These cells contain nutritive substances. The tapetal layer maintains its identity throughout the life of the sporangium. The sporogenous cells separate and round off to form **spore mother cells** (Fig. 4.11, G) which undergo meiosis. The tetrads are tetrahedral and after secreting their own walls they separate into spores. The number of spores per sporangium varies considerably.

Development of the Sporangium (Fig. 4.11, A–G)

The sporangium in ***L. selago*** originates from a single transverse row of superficial cells (Fig. 4.11, A, B) on the dorsal or upper surface of the sporophyll near its base or close to its point of attachment with the stem. In a radial section only one of the cells in a row is visible and it appears as if the sporangium develops from a single cell. As a matter of fact, all the cells in this transverse row take part in the development of the sporangium. Each of these cells divides periclinally to form a middle row of **archesporial cells** (Fig. 4.11, B, C, D) covered by a single row of **primary wall cells** above and a row of cells below (Fig. 4.11, C). In a median radial section (Fig. 4.11, B) this stage shows a row of three cells; (***i***) an upper cell which contributes to the sporangial wall (primary wall cell), portion or whole of the sporangial stalk and part of the tapetum, (***ii***) a middle cell which is archesporial in nature, and (***iii***) a lower cell that contributes to the **tapetum** in the lower or the basal region of the sporangium. This lower cell as it appears in median radial section or a row of lower cells as they appear in a tangential section constitute the **sub-archesporial cells**. Since the sporangium originates from a group of cells the development is of the **eusporangiate** type.

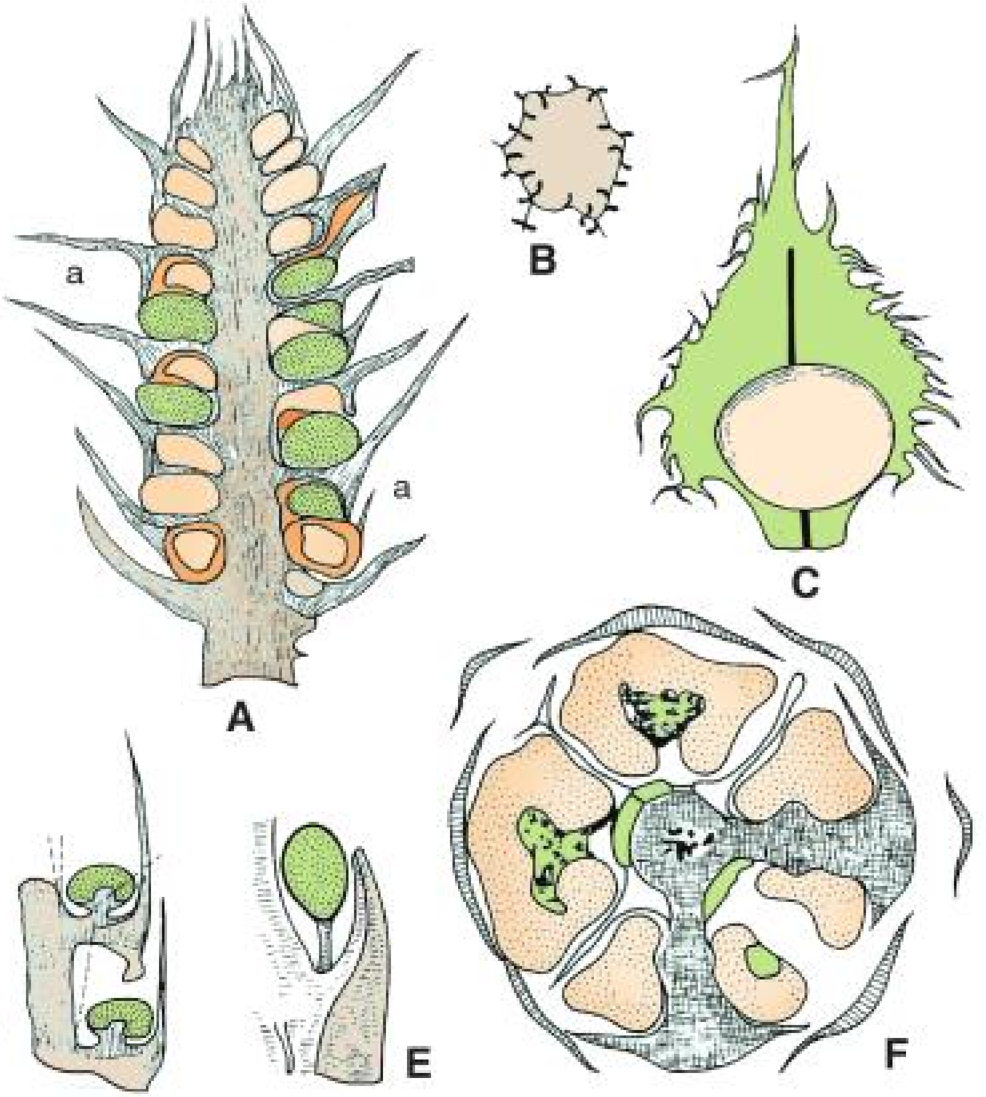


Fig. 4.10 (A–F). A. ***Lycopodium cernuum*** longitudinal section of strobilus: *a*, band of lignified cells; B. ***L. cernuum.*** Cell from sporangium wall; C. ***L. cernuum.*** Sporophyll and sporangium ; *It*, vascular bundle; D. ***L. clavatum.*** Part of radial longitudinal section of strobilus ; *P*, sterile tissue; E. ***L. phlegmaria.*** Sporophyll and stalked sporangium; F. ***L. clavatum.*** Transverse section of strobilus ; *p*, sterile pad, a,b,c,d, sporangia (After Seward, 1910).

The primary wall cells undergo periclinal and anticlinal divisions to form a three or more layered thick sporangial wall. The inner-most layer of wall is differentiated as the **tapetum.** Its cells are prominent and contain stored food material. This layer provides nutrition to the developing sporogenous tissue. The tapetum in the basal region of the sporangium differentiates from the subarchesporial cells. The tapetal layer in ***Lycopodium*** remains intact and does not undergo disorganisation to form the **periplasmodial** fluid. It has been observed that in ***L. selago*** and other species the outer wall cells of the maturing sporangium elongate anticlinally and develop thickenings on their inner and radial walls. The inner wall layers break down completely or nearly so, so that the mature sporangium has only an outer thickened wall. The tapetum and some of the non-functional spore mother cells also disorganise to form a fluid mass or nutritive fluid in which the spores lie free.

The **archesporial cells** whose number is not constant, although it is seven in most of the developing sporangia of ***L. selago*** divide in various planes to form a group of cells called the **sporogenous tissue**. These cells then grow in size, round off and separate from one another to form **spore mother cells** or **sporocytes**. The sporocytes undergo meiosis and produce **tetrahedral tetrads** of haploid spores. These finally separate and secrete a wall whose ornamentation varies with species. The fully grown sporangium is more or less reniform and possesses a short stalk.

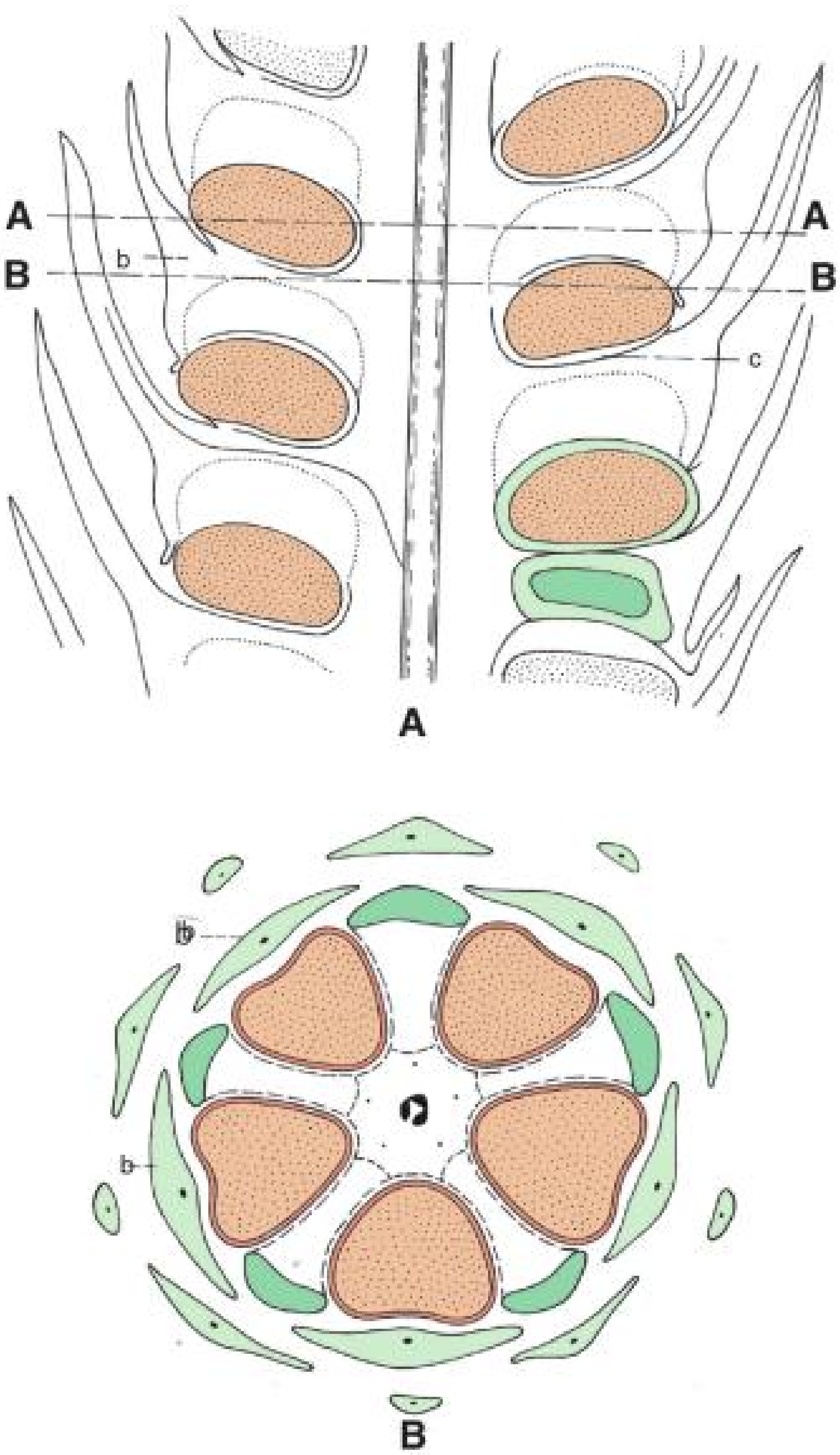


Fig. 4.10a (A-B). *Lycopodium cernuum*. **A.** Radial longitudinal section of the cone. Note the massive stalk (*c*) and foliar nature of the sporangium; **B.** T.S. of A at the level A-A (After Lang)

Lycopodium selago shows the type of sporangial development that can be regarded as characteristic for the section ***Urostachya***. There are, however, differences in the number of cells in the archesporial row and in the number of layers in the sporangial wall. In ***L. dichotomum*** the sporangial wall is 4-7 layers thick.

In ***L. inundatum*** which belongs to ***Rhopalostachya*** there are two tangential rows of archesporial cells as compared to one in ***L. selago***.

However, in ***L. clavatum***, and ***L. alpinum***, both of which belong to ***Rhopalostachya*** group there are three tangential rows of archesporial cells. The sporangium thus is more massive. In these species the **subarchesporial** pad is comparatively well developed and extends in between the sporogenous tissue as small processes. The sporangial stalk is thick and short as compared to the long and narrow stalk in ***L. selago***. Bower regarded ***L. inundatum*** as an intermediate form linking the two types of sporangial development in ***L. selago*** and ***L. clavatum***.

Dehiscence of Sporangium

In species with compact strobili the dehiscence of the sporangium is preceded by elongation of the internodes of the central axis. As a result the sporophylls spread out and expose the sporangia. The sporangia dehisce along a line of cells running across the upper surface of the kidney-shaped sporangium. This line of cells is differentiated in the outermost layer of sporangial wall and may be designated as the **stomium**. The inner walls of the cells constituting the stomium are thick and lingified. The cells making up the bulk of sporangial wall, other than the stomium have their side walls thickened only. As the exposed sporangia lose water and dry, a condition of stress and strain develops in the cells of the sporangial wall. These stresses lead to the appearance of a slit in the stomium and cause the sporangial wall to split open from top to the base of the sporangium in the form of two valves. The loose spore mass projects out of the open slit. The air currents scatter the spores and disseminate them.

GAMETOPHYTE

It starts with the spore that germinates to give rise to a new individual called the **gametophyte** or the **prothallus**.

Structure of the Spore

Lycopodium is homosporous. The spores are unicellular and range in diameter between 0.03—0.05 mm. The spores occur in tetrahedral tetrads and hence have a tetrahedral shape with a rounded or semicircular base (Fig. 4.1, D, E). Each spore has a triradiate ridge and is enclosed within a thin or thick spore wall. The spore wall has two layers (***Afzelius et el***, 1954). The inner layer as revealed by ultramicroscope studies is granular and is surrounded by an outer layer which is made up of concentric lamellae. Each spore has a single haploid nucleus surrounded by cytoplasm which is filled with reserve food material (fats and oils). The chloroplasts may or may not be present.

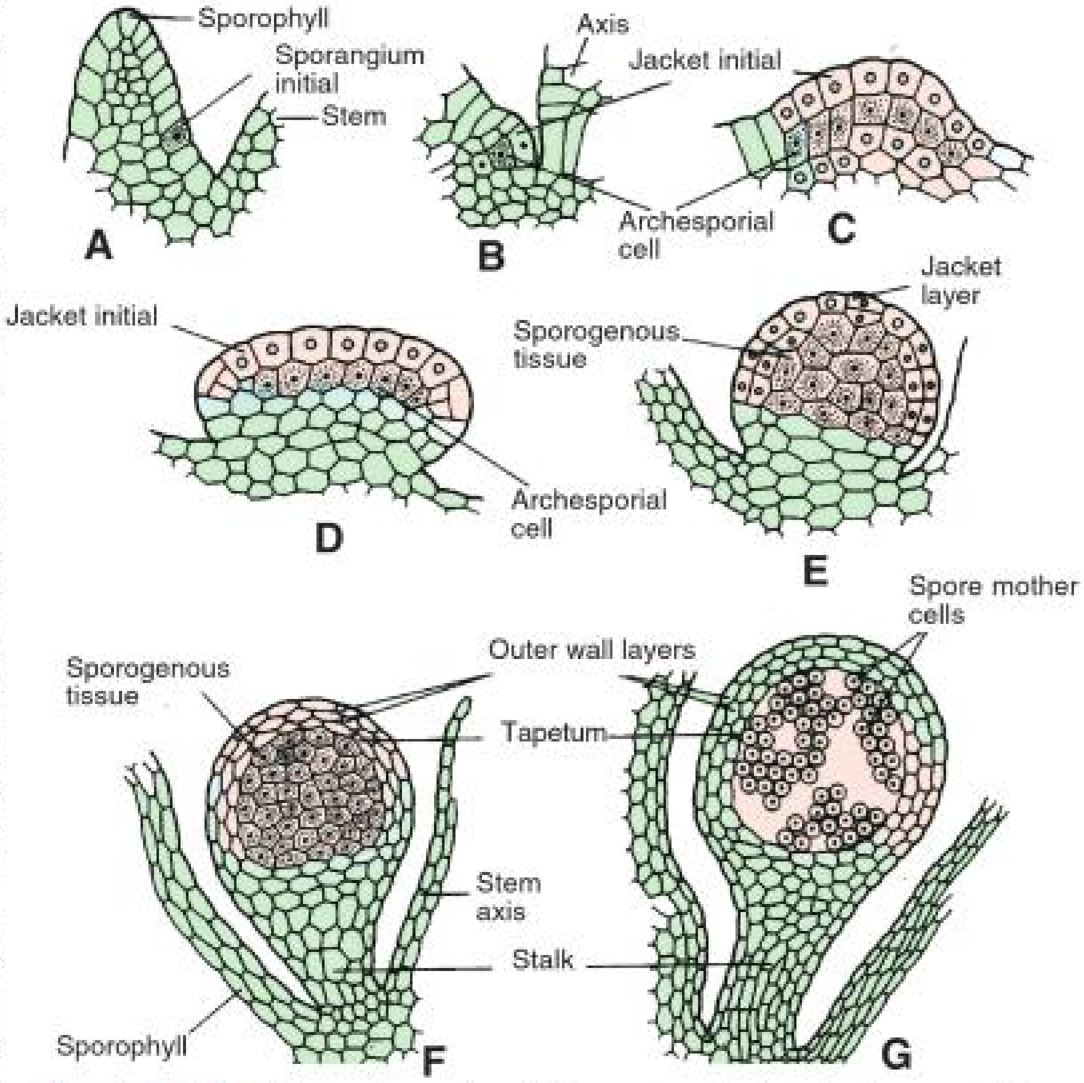

Sporophyll
Sporangium initial
Stem
A
Axis
Jacket initial
B
Archesporial cell
C
Jacket initial
D
Archesporial cell
Sporogenous tissue
Jacket layer
E
Spore mother cells
Sporogenous tissue
Outer wall layers
Tapetum
Stem axis
Stalk
Sporophyll
F
G

Fig. 4.11 (A-G). ***Lycopodium selago.*** Various stages in the development of sporangium. For explanation see text (After Bower)

The spore wall may be smooth or it may be variously sculptured (Fig. 4.1, D, E). Sculpturing may be in the form of pits or reticulate ridges as in ***L. complanatum***, ***L. clavatum*** (Fig. 4.1, D, E). In ***L. selago*** and ***L. phlegmaria*** the outer spore wall is beset with rounded or peg-like outgrowths. In ***L. inundatum***, ***L. cernuum*** and some other species the outer layer of the spore wall is thrown into slightly raised ridges that alternate with shallow grooves. In some species of ***Lycopodium*** the spore wall is thick and cutinised.

The spores of ***Lycopodium*** are used as reducing agents in gunpowder. They are also used as coating for pills.

Germination of the Spore (Fig. 4.12, A–F)

The time taken by the spores to germinate varies from a few days after their liberation from the sporangium to several years (3 to 8 years). This unusual delay in germination of spores has been attributed, by some workers (Bruchmann ; Barrows, 1935) to their thick and cutinised walls. In case the spores germinate within a few days of their liberation from the sporangium, they produce aerial short-lived and green prothalli, ***e.g. L. cernuum*** and ***L. inundatum***. In case the spores take a longer time to germinate, they get buried under the soil and produce colourless and subterranean prothalli that are comparatively large and tuberous and long-lived, ***e.g.***, ***L. clavatum***, ***L. complanatum***, ***L. obscurum*** and ***L. annotinum.***

There is great variation in the genus regarding the details of spore germination. The usual steps that lead the spore to the formation of mature prothallus are outlined below:

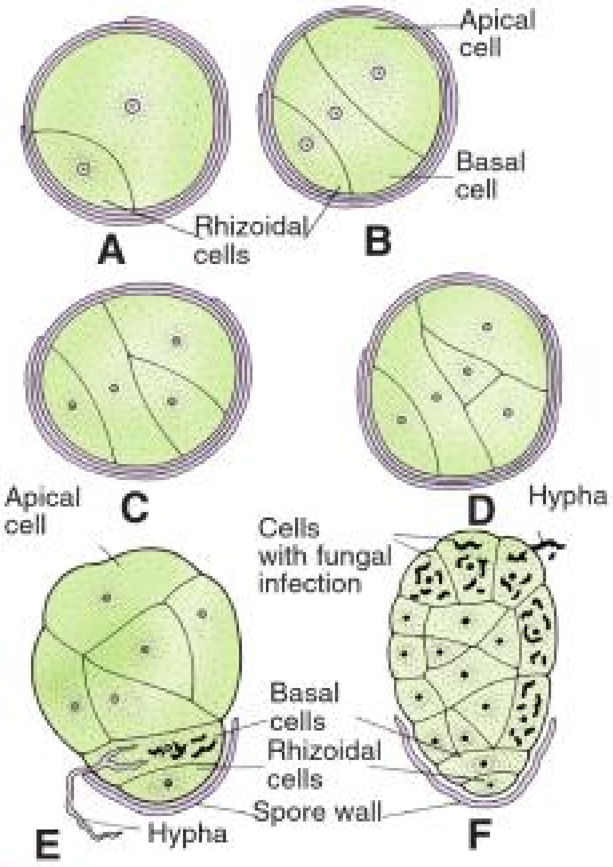


Fig. 4.12. *Lycopodium annotinum.* Various stages in the germination of the spore. (After Bruchmann)

The spores germinate under moist conditions. They absorb water and swell up. Before the spore wall ruptures along the triradiate mark, the contents of the spore have already divided into two unequal cells. One of these cells is small and lenticular or biconvex and lies under one of the three arms of the triradiate mark. The rest of the spore is occupied by the larger cell. The smaller is called the **rhizoidal cell** and takes no further part in the development of the prothallus. It is colourless. At this stage the spore wall ruptures at the triradiate mark and the two-celled prothallus projects out. Further division taken place in the larger cell. It soon divides by a vertical or an oblique second wall into two cells. The second division which divides the larger cell into two cells differentiates the **basal cell** lying next to the **rhizoidal cell** and the third cell (Fig. 4.12). At this stage the young prothallus has three cells. These are the **rhizoidal cell,** the **basal cell** and the **upper cell.**

The third cell divides further by two successive divisions to differentiate an **apical cell** with two cutting faces (Fig. 4.12, E). This is the five-celled stage of the young prothallus. At this stage the cells are devoid of chloroplasts and endophytic fungus. In the species destined to produce aerial, green prothalli, the rest of the stages leading to the formation of a mature prothallus are completed within the season depending upon the attack of the mycorrhizal fungus. In case the mycorrhizal fungus fails to enter the five-called prothallium, further growth is arrested and the young prothallus may die. In the species with subterranean prothalli, further growth stops at the five-celled stage. A resting period of about a year intervenes between this stage and further development. During this interval the mycorrhizal infection takes place (Fig. 4.12, E, F). This infection takes place through the **basal cell** (Fig. 4.12, E, F) and it is believed that physiologically, the fungus supplies certain substances vital for the proper development of the prothallus. Further growth is resumed and is marked by the activity of the apical cells which cut off six-segments. Later the apical cell is replaced by a group of meristematic cells. These cells divide repeatedly and contribute to the further development of the prothallus.

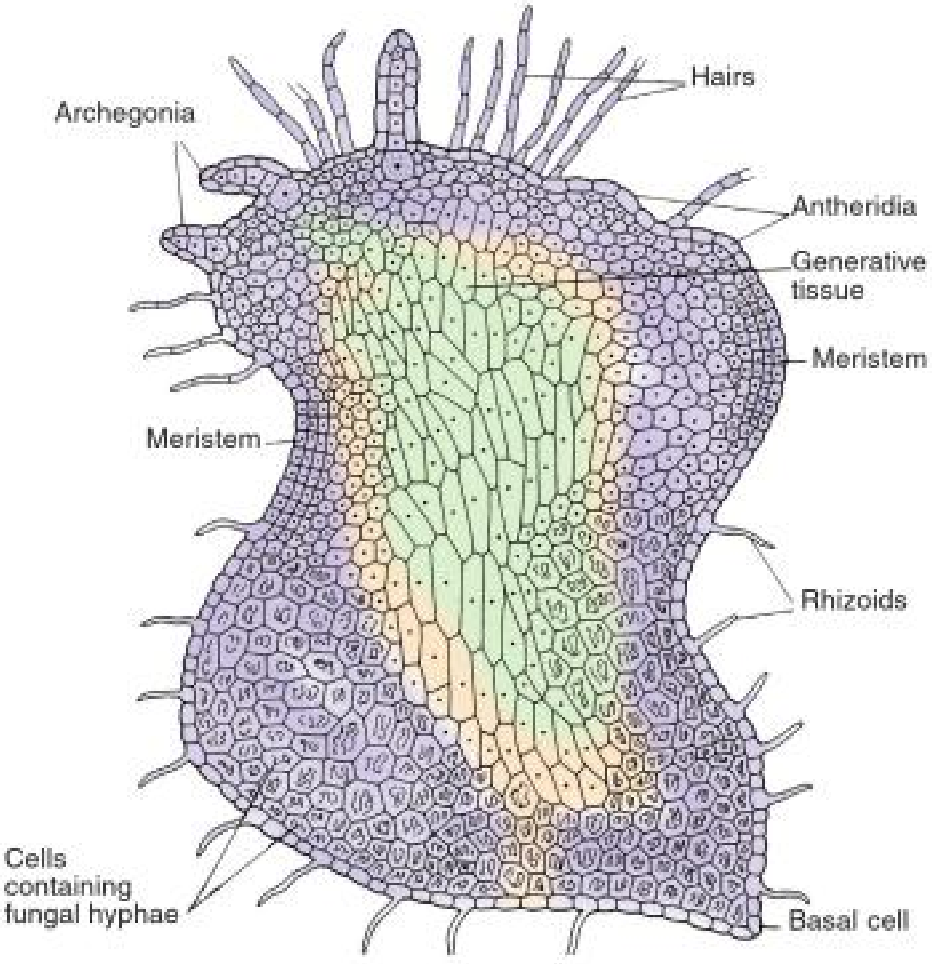


Fig. 4.13. ***Lycopodium selago.*** A mature prothallus showing details of internal structure. The generative region bears antheridia and archegonia (After Bruchmann)

Wetmore and Morel (1951) cultivated the spores of ***L. cernuum*** in culture solution containing minerals and glucose. The spores first develop chloroplasts and later divide into two unequal cells. The smaller remains inactive and the larger divides by oblique walls to cut off a two-sided apical cell, which cuts off segments to form a mass of undifferentiated cells called the **primary tubercle**. Further development is arrested here and continues further only if an endophytic fungus attacks the cells. Resumption of further growth results in the characteristic shape of the prothallus of ***L. cernuum***. It takes six months under controlled conditions.

Structure of Mature Prothallus

The structure of the mature prothallus, in various species of ***Lycopodium***, was described by Treub (1884, 1889) and Bruchmann (1898–1916). As a result of their studies three intergrading types of prothalli have been discovered. These three types will be discussed in detail.

First Type

It is exemplified by ***L. cernuum*** and ***L. inundatum***. The prothallus in ***L. cernnum*** (Fig. 4.17, A–E) has an erect cylindrical body only two to three millimeters long. It grows at the surface of the ground and consists of a colourless basal portion buried in the soil and a conspicuously lobed aerial crown that is green and bears sex organs at the bases of the green lobes. The rhizoids are restricted to

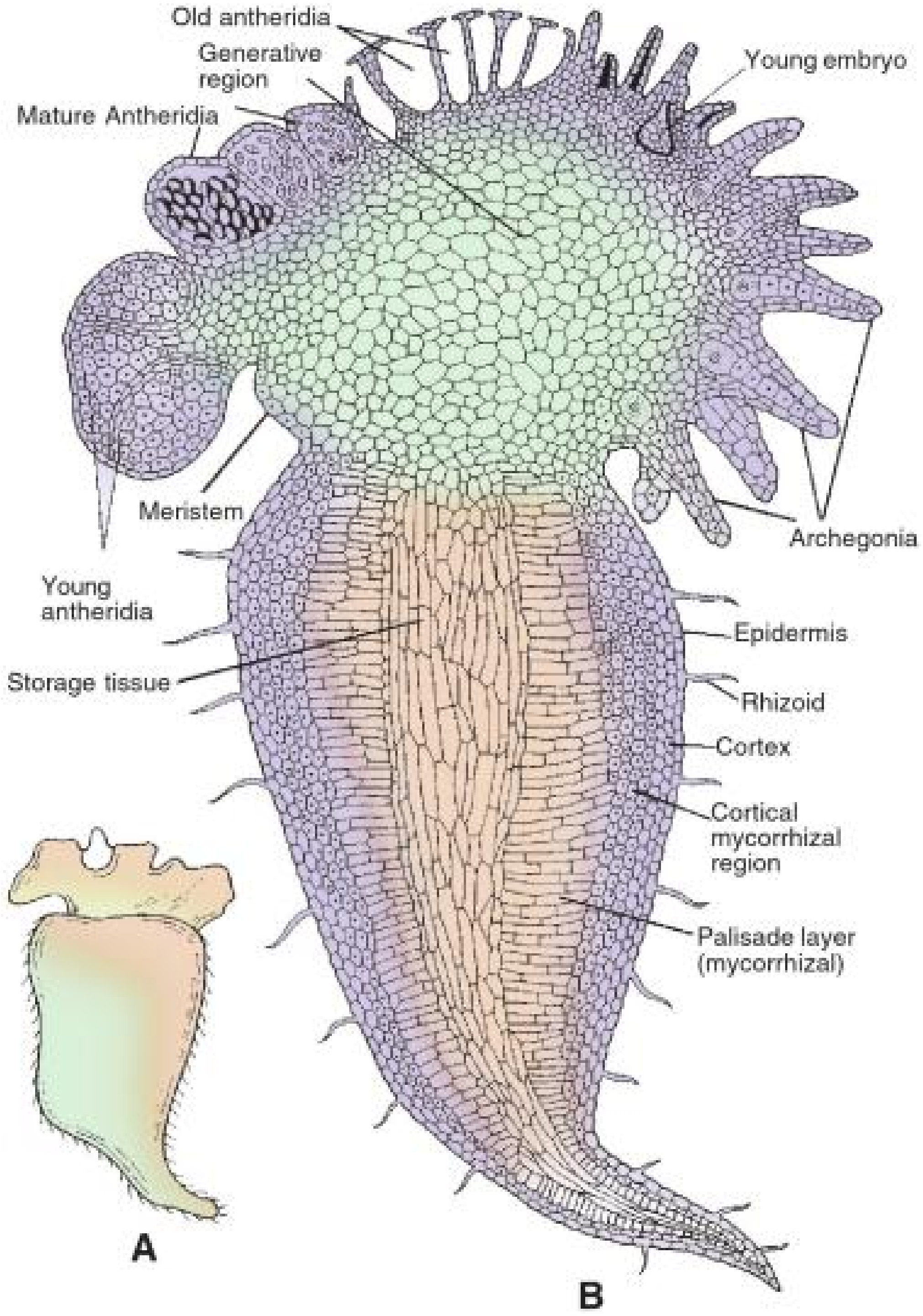

Old antheridia
Generative region
Mature Antheridia
Young embryo
Meristem
Archegonia
Young antheridia
Epidermis
Storage tissue
Rhizoid
Cortex
Cortical mycorrhizal region
Palisade layer (mycorrhizal)
A
B

Fig. 4.14 (A-B). ***Lycopodium complanatum.*** **A.** A mature prothallus; **B.** Section of a mature prothallus showing details of internal structure. (After Bruchmann).

the lower buried portion which also contains an endophytic fungus. This prothallus is independent because it manufactures its own food. The prothallus of this species reaches maturity within six months and grows by means of a meristematic zone that is present below the apex and is marginal in position. It forms a rim around the cylindrical upper part of the prothallus. The sex organs develop from cells cut off by the meristem and the youngest is present near the meristem. The portion of prothallus bearing the sex organs is called the **generative zone**. This zone is green and is made up of undifferentiated parenchymatous cells, which are devoid of fungal hyphae.

Second Type

This type includes subterranean prothalli that have acquired a saprophytic mode of nutrition. It is represented by ***L. complanatum*** (Fig. 4.14), ***L. clavatum*** (Fig. 4.15), ***L. annotinum*** and ***L. obscurum***. The prothalli in all these species are tuberous, yellowish brown or even colourless. They store sufficient food material and vary in dimensions from 12 to 18 mm. long. Their shape also varies and may be top-shaped (***L. clavatum***), carrot-shaped or conical (***L. complanatum***) and discoid. They have two distinct regions : (***i***) the lower conical region, and (***ii***) the upper broad **generative region**. The conical region shows distinct zones. The outermost layer of cells resembles epidermal tissue and bear numerous rhizoids. Next to it is the several layered **cortical zone** which is composed of tightly packed parenchymatous cells that are filled with the endophytic fungal hyphae. Next to this zone is the **palisade zone** which is made up of closely packed columnar cells that also contain hyphae (Fig. 4.14). Next to this is the **central storage zone** whose cells are filled with stored food (Fig. 4.14). The upper broad region of the prothallus is called the **generative region** and is a broad expanse of parenchyma cells unaffected by endophytic fungus. It has a marginal meristem (Figs. 4.14 and 4.15) and bears sex organs on its flattened surface. The archegonia are found near the margins and the antheridia are located centrally. In ***L. complanatum*** (Fig. 4.14) the upper broad region is irregularly lobed and bears sex organs. In *L.* ***clavatum*** the upper generative region is irregularly cup-shaped (Fig. 4.15) with a depressed centre surrounded by a broad rim. In ***L. obscurum*** De Maggio (1967) induced the formation of tracheids in the prothallus.

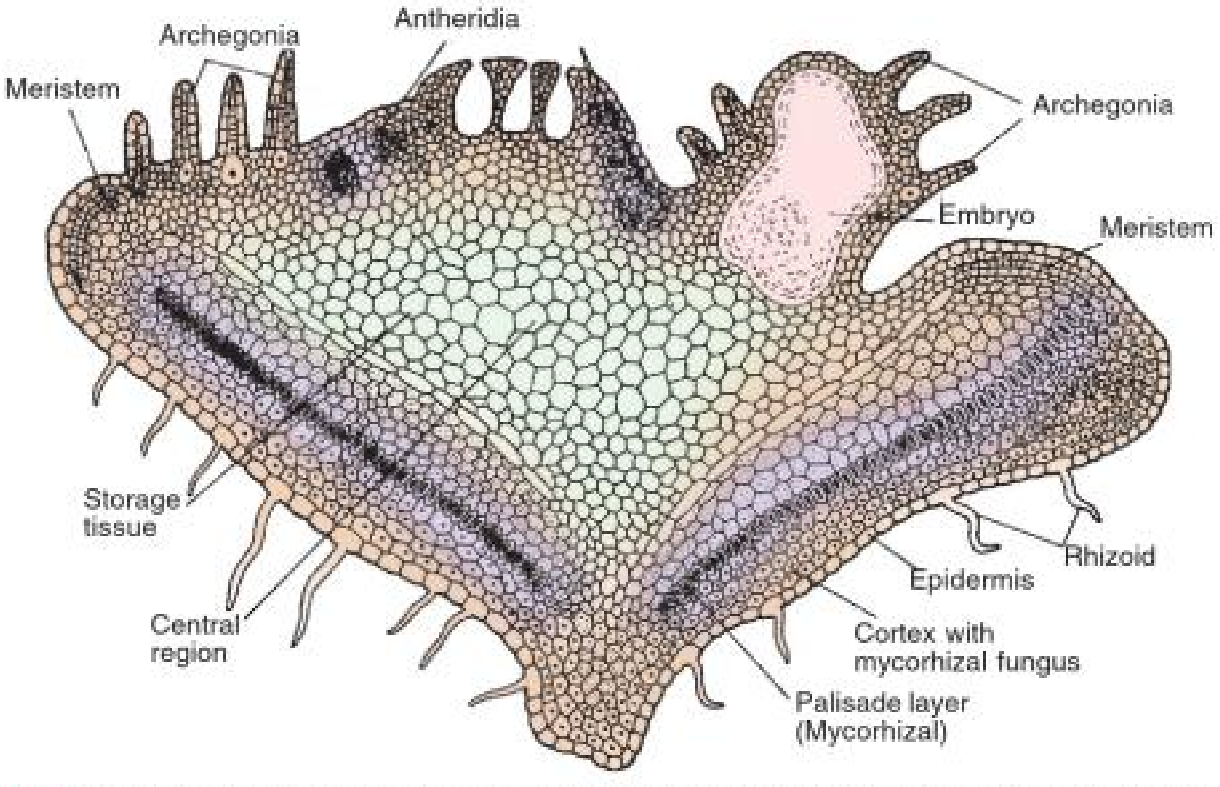


Fig. 4.15. *Lycopodium clavatum.* Section through the prothallus showing detailed internal structure. (After Bruchmann)

Misra (1978) described the geophilous gametophytes of ***L. serratum*** that are cylindircal to ovoid in shape and brownish in colour. They are monoecious and saprophytic. The endophytic fungus in this species is not restricted to any special region but is found throughout the cells of the prothallus.

Third Type

This type includes colourless, subterranean, saprophytic and repeatedly branched monopodial prothalli that are found only in the epiphytic species of ***Lycopodium***. The typical type is represented by ***L. phlegmaria*** (Fig. 4.16, A—C). The prothallus grows in the humus collected on the branches of the trees. The branches arise irregularly and ramify into the dead bark. The prothallus is attached to the substratum by means of absorbent rhizoids that grow in all directions. The growth of the prothallus and its branches is apical and takes place by the activity of two prismatic initial cells that lie side by side. In this case the endophytic fungus is found in the inner core of cells. These cells also store oil as reserve food. This centrally located mycorrhizal region is surrounded by one or more layers of cortical cells that are devoid of endophytic fungus and are colourless. The rhizoids arise from the outermost layer. The prothallus is marked by unlimited apical growth followed by progressive death and decay of older regions. This leads to fragmentation and thereby to vegetative propagation of the prothallus. The branches also bear, near their apices shortly stalked and multicellular bodies called the **gemmae** (Fig. 4.16, C). They get easily detached and can germinate to produce new prothalli. The sex organs are borne on the upper surface of the branches and are always intermingled with paraphyses. The branches bear both antheridia and archegonia but antheridia always develop first.

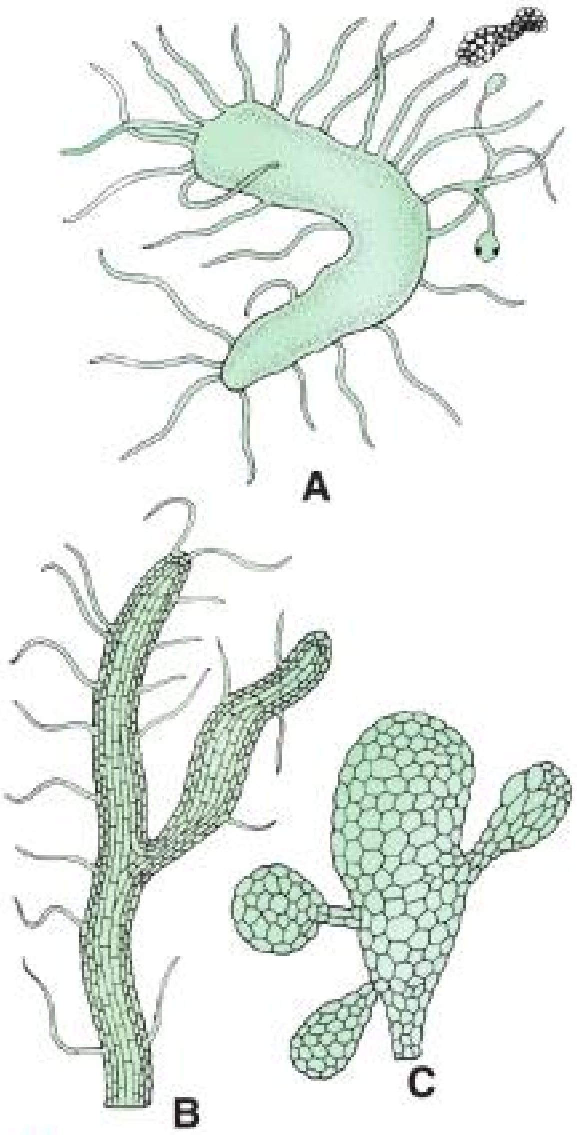


Fig. 4.16 (A-C). *Lycopodium phlegmaria*. **A.** Mature prothallus covered with numerous filamentous outgrowths; **B.** A sterile prothallus; **C.** A gemma bearing secondary gemmae. (After Gobel)

The prothallus in ***L. selago*** may be subterranean or epiterranean (aerial). In case the spores of this species germinate soon after their liberation and are not buried under the soil, they give rise to an aerial and photosynthetic prothallus. If the spores are buried under the soil they give rise to a pale and a subterranean prothallus. The form of the underground prothallus depends upon the depth and character of the soil. If the soil is firm, the prothallus is elongated and cylindrical in form. In an open and loose soil the prothalli are compressed and flattened and taper below into a conical point (Fig. 4.13). The upper region is broad and cup-shaped and bears sex organs. It is also called the **generative zone** and lacks endophytic fungus. It is lobed and the lobes bear sex organs on their side facing inwards. The outer side bears rhizoids alone. This indicates a feeble transition to dorsiventrality. The meristematic zone occupies the margin of the cup. **Mycorrhizal zone** is confined only to the lower conical region. The rhizoids cover the entire surface and arise from an outer layer called the epidermis (Fig. 4.13). The cells containing endophytic fungus also store food material. The antheridia are borne in a regular sequence from the centre to the marginal meristem and are followed by archegonia. The lobes bearing the sex organs also bear paraphyses. The underground prothalli of ***L. selago*** when growing near the surface of the soil may emerge out partly and become green in colour. Such prothalli are partly colourless and partly green. So we derive the following conclusions from the study of the prothallus of ***L. selago***:—(***i***) they are green and photosynthetic when aerial. (***ii***) they may be partly green and partly colourless or they can be partly subterranean and partly epiterranean. (***iii***) their form may be obconical below and flat and lobed above as in prothalli growing in loose soil. (***iv)*** they assume a cylindrical form in firm soil and when growing in rotten wood they give out branches that show a dorsiventral symmetry. (***v***) they exhibit both holophytic and saprophytic nutrition. (***vi)*** the aerial region of the thallus is lobed.

The subterranean gametophytes of ***L. selago*** resemble the gametophytes of epiphytic species like ***L. phlegmaria*** and ***L. billardieri*** in possessing slender and cylindrical branches and in the presence of paraphyses among the sex organs. The underground prothallus of ***L. volubile*** which is very much like that of ***L. clavatum*** resembles ***L. selago*** in that it sometimes emerges out of the soil and develops chlorophyll. ***L. clavatum***, ***L. complanatum***, ***L. annotinum***, ***L. volubile*** and other subterranean species have at least of a few common stages in their ontogeny with that of ***L. selago***. These are: (***i***) the presence of a two-sided apical cell in the earlier stages of development; (***ii***) further development depending upon the attack of endophytic fungus; (***iii***) formation of a meristematic zone whose position is marginal; (***iv***) the obconical or conical shape of the lower region; and (***v***) presence of lobes in the upper region. The prothalli of all these subterranean species resemble with that of ***L. selago*** in their saprophytic mode of nutrition.

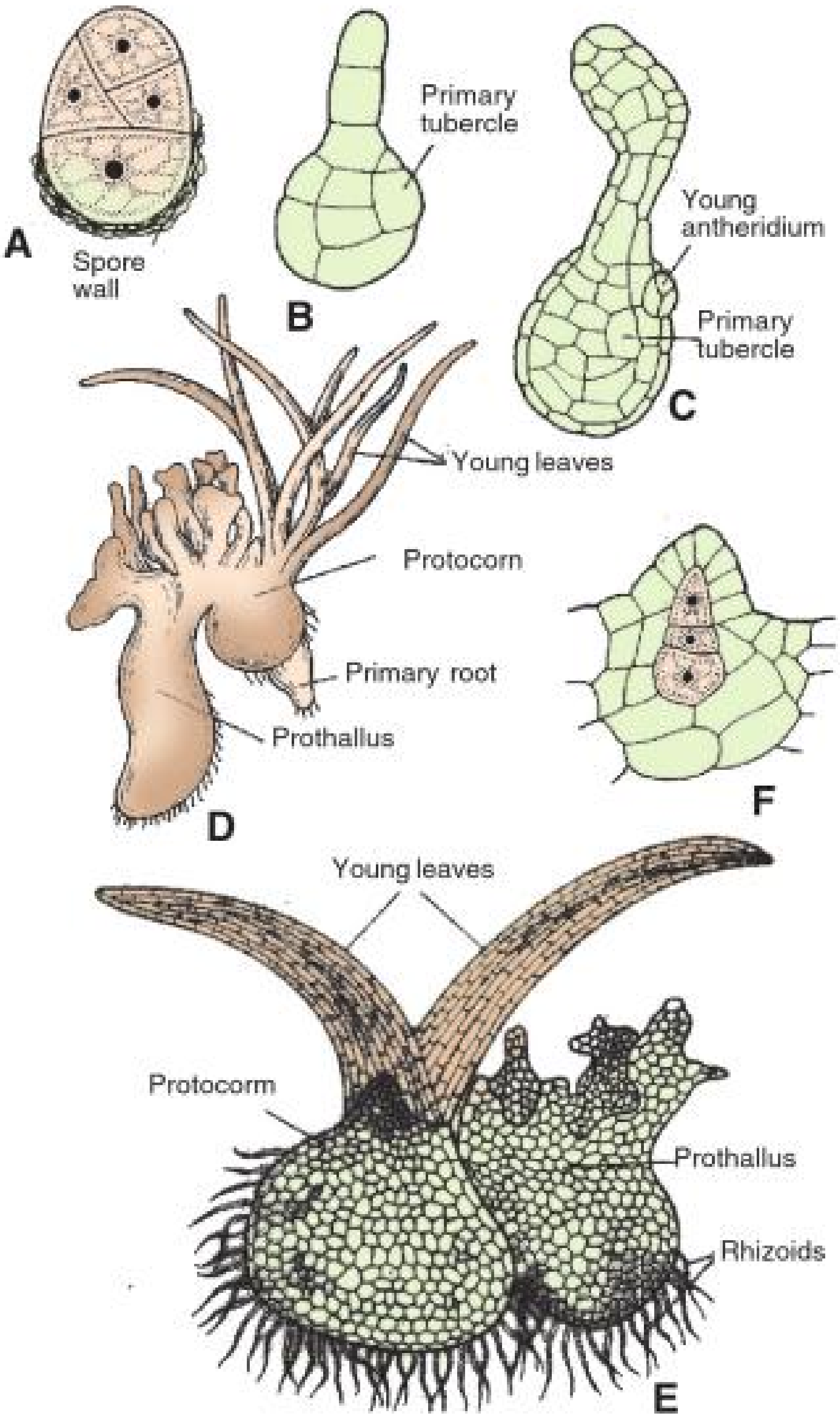


Fig. 4. 17 (A–E). ***Lycopodium cernuum.*** Gametophytic generation. **A, B.** Younger stages of development; **C.** An older stage with the first antheridium; **D.** A mature prothallus with attached young sporophyte; **E.** The same as D; **F.** A mature archegonium. (After Treub).

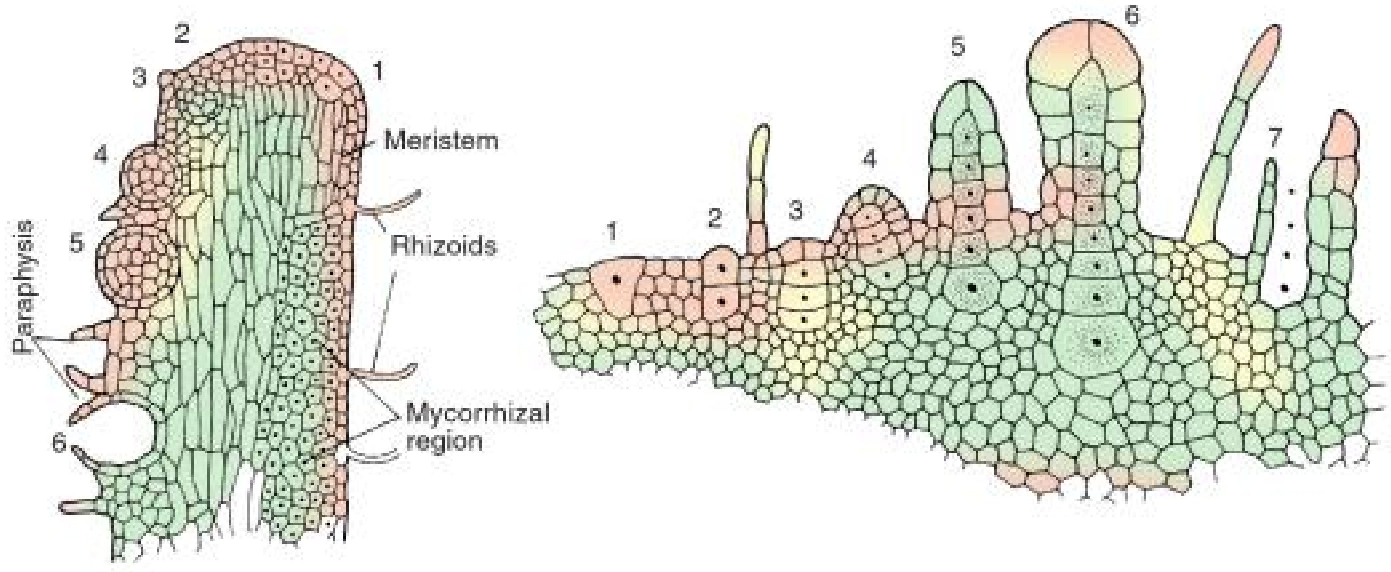


Fig. 4.18. *Lycopodium selago.* Sex organs. Left side :– Median L.S. of prothallus showing stages in antheridial development. Right side :– L.S. prothallus showing archegonia in various stages of development. (After Bruchmann)

The aerial prothalli of ***L. cernuum***, ***L. inundatum*** and ***L. salakense*** resemble that of aerial prothalli of ***L. selago*** in several respects. The common features bearing :—(***i***) Their autophytic mode of nutrition. (***ii***) Their green colour. (***iii***) Presence of lobes in the upper distal region. (***iv***) Rhizoids restricted only to the lower conical region. (***v***) The mycorrhiza also restricted to the lower conical portion and is distributed in much the same manner. (***vi***) Presence of sex organs in the upper lobed region. (***vii***) Earlier stages of development and presence of meristem.

It becomes clear from the above account that prothallus of ***L. selago*** bears resemblances to all the three types of prothalli of ***Lycopodium***. It can, therefore, be regarded as an intermediate type which links together the three types of prothalli. Such a link has been pointed out by Lang (1899), Campbell (1939), and Bower (1935). Manton (1950) studied the cytology of four British species of ***Lycopodium*** and as a result she came to the conclusion that ***L. selago***, ***often*** considered to be a central and primitive type is found on cytological evidence, to be a hybrid of very high chromosome number.

Freeberg and Wetmore (1957) were able to grow spores of some species with subterranean gametophytes on a cultural medium containing only mineral nutrients and sucrose. The spores (after scarification or acid treatment) germinated into masses of callus tissue with erect lobes that were slightly green in colour. Such prothalli bear normal sex organs and resembled very much those of ***L. cernuum***.

Vegetative Propagation of the Prothallus

1. **By the formation of gemmae** (Fig. 4.16, C). They are borne on the branches of the prothallus in ***L. phlegmaria*** and arise singly or in clusters near the tips of the branches. A gemma develops from a single superficial cell of the branch and is usually a large club-shaped and shortly stalked structure. In starved prothalli the gemmae are few celled and thick-walled and their cells store food material. They are capable of perennating and germinate into new prothalli on the advent of favourable weather.
2. **By the progressive decay of the older parts** of the prothallus and thereby separating the younger branches, which behave as individual prothalli (***L. phlegmaria*** and ***L. billardieri***).
3. In ***L. inundatum*** adventitious buds arise from the injured parts of the lobes.

Sex Organs

The exosporic gametophytes of ***Lycopodium*** are essentially monoecious but protandrous. The antheridia and archegonia, in most of the species of ***Lycopodium***, are formed in distinct patches or clusters on the upper surface of the prothallus. In ***L. lucidulum*** Spessard (1922) reported intermingling of the antheridia and archegonia.

Antheridia

The antheridia in ***Lycopodium*** develop earlier than the archegonia and the youngest lie near the marginal meristem. In ***L. lucidulum*** there is intermingling of the two kinds of sex organs. The antheridia are mostly embedded (Fig. 4.18, 4.19) in the tissue of the prothallus.

Development (Fig. 4.18 and 4.19)

The antheridium arises from a single superficial cell which divides by a transverse wall into an outer **primary wall cell** and an inner **primary spermatogenous cell**. The **primary wall cell** divides by anticlinal wall to form a one-layered wall or the jacket of the antheridium. A triangular **opercular cell** is ultimately differentiated in the middle of the jacket layer and marks the point of exit of spermatozoids. The **primary spermatogenous cell** divides repeatedly to give rise to a mass of androgonial cells. The **androgonial cells** divide further and give rise to a mass of **spermatocytes** or **androcytes** or **sperm mother cells** (Fig. 4.19, E) whose number varies considerably. In ***L. phlegmaria*** a single section of the antheridium contains up to two hundred **spermatocytes**. The development of spermatozoid within the spermatocyte has not been studied in detail.

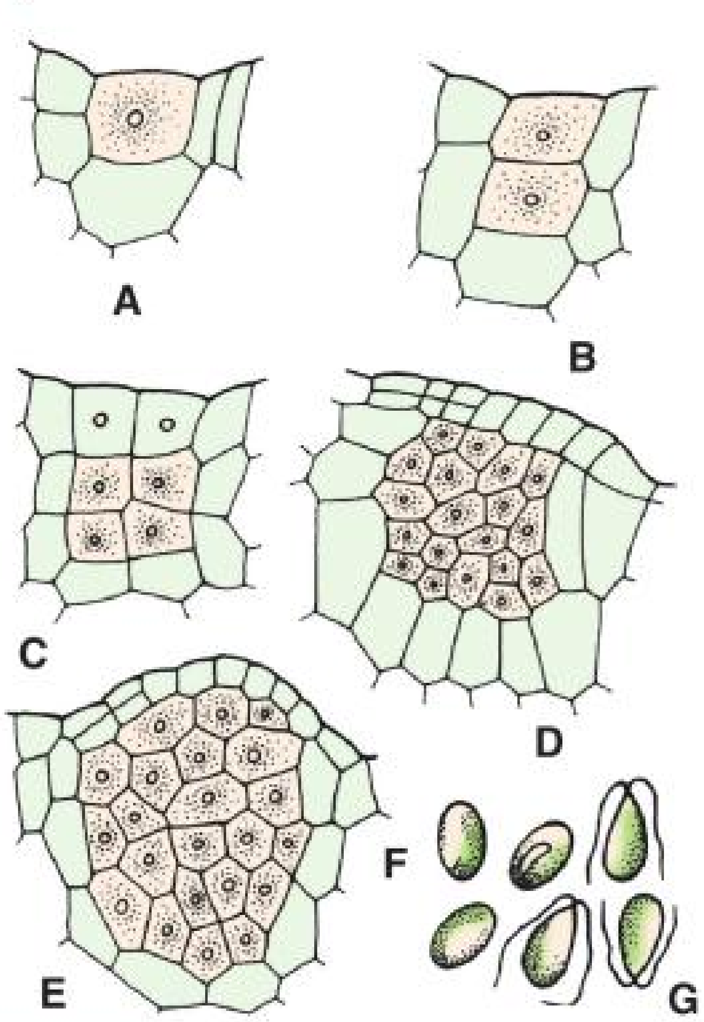


Fig. 4.19 (A–G). *Lycopodium clavatum*. A–E. Various stages in the development of antheridium; F. Spermatocytes; G. Spermatozoids. (After Bruchmann)

Bruchmann has studied the structure of the spermatozoids in ***L. clavatum***. It is oval in shape (Fig. 4.19, G) and about twice as long as broad. It is pointed at the anterior end which bears two flagella. The cytoplasm forms the major portion of the spermatozoid and the nucleus lies on one side. It is interesting that unlike all other pteridophytes the nucleus in the spermatozoids of ***Lycopodium*** does not form a major part of its body. In this respect it resembles the male gametes of some algae. Spessard (1922) studied the spermatozoids of ***L. lucidulum*** and described the nucleus as elongated and curved. Treub described the spermatozoids of ***L. phlegmaria*** as elongated and twisted.

Structure of Mature Antheridium (Fig. 4.18 and 4.19, E)

A mature antheridium is either completely embedded in the tissue of the prothallus (***L. selago***) or slightly projecting. It has a single-layered antheridial wall with a distinct triangular **opercular cell**. The wall encloses a large number of spermatocytes whose protoplasts metamorphose into biflagellate spermatozoids.

It dehisces by the mucilaginisation of the single opercular cell or a group of jacket cells. The spermatocytes containing spermatozoids absorb water, swell up and cause the rupture of the antheridial wall.

Archegonia (Fig. 4.18 and Fig. 4.19 a)

Development. The archegonial initial is superficial. It divides by a periclinal wall into an outer **primary cover cell** (Fig. 4.18, 2, Fig. 4.19_a B) and inner **central cell**. The **primary cover cell** divides by two intersecting walls into (Fig. 4.18, 3) four **neck initials** which divide further by transverse walls to give rise to the neck that varies from three to many cells in height. (Fig. 4.19_a D–F). The neck is composed of four longitudinal rows. The **central cell** divides by a transverse wall into an upper **primary canal cell** and a lower **primary ventral cell** (Fig. 4.18, 3 and 4.19_a D). The former may function directly as a single **neck canal cell** in the archegonia of aerial prothalli or it may divide repeatedly by transverse divisions to form a variable number of neck canal cells (Fig. 4.19_a E). In ***L. selago*** there may be up to seven neck canal cells (Fig. 4.18, 6 and 4.19_a F). In ***L. complanatum*** there are 14 to 16 neck canal cells. Freeburg and Wetmore (1957) cultured the prothalli of these two species and reported that the archegonia under cultural conditions have very short necks and only one **neck canal cell**. The primary **ventral cell** undergoes a transverse division to form a lower egg cell and an upper **ventral canal cell** (Fig. 4.18, 5). In some cases the **primary ventral cell** does not divide and becomes slightly broader and functions directly as the egg cell. Its cytoplasm and nucleus form the female gamete or the **egg** or the **oosphere.**

Structure (Fig. 4.18 ; 4.17, F)

A mature archegonium is distinguishable into a slightly broader and embedded lower portion called the **venter** and a projecting part called the **neck**. The length of the neck varies considerably in the genus. The longest neck is found in ***L. complanatum*** (Fig. 4.14) and ***L. selago*** (Fig. 4.18, 6). Spessard (1922) reported that species with subterranean prothalli bear long necked archegonia. The neck is usually made up of 4 rows of cells, each row 3 to several cells high; five longitudinal rows of neck cells have also been reported and such archegonia have very long necks (***cf.***, bryophyte archegonia). The neck encloses a neck canal which contains one to 16 neck canal cells. The venter has a ventral canal cell and an egg cell. The venter has no wall of its own but is protected and surrounded by the tissue of the prothallus.

Dehiscence

The archegonium when mature dehisces by the disorganisation of the **neck canal cells** and the **ventral canal cell** and opening the uppermost tier of the neck cells. This creates an open passage for the spermatozoids to enter the neck and reach the **oosphere.**

Fertilisation

It is affected in the presence of water through which the biflagellate spermatozoids swim and reach the open archegonial necks. Bruchmann (1909) reported that the spermatozoids are attracted by a chemical stimulus. He stated that the archegonial necks secrete free citric acid or its salts whose smell attracts the spermatozoids. Only one spermatozoid is able to reach the egg and effect fertilisation. The male and female nuclei fuse together (syngamy) and form a diploid fusion nucleus. So the act of fertilisation switches on the diploid generation. The diploid nucleus with its surrounding cytoplasm and a wall is called **the ospore.**

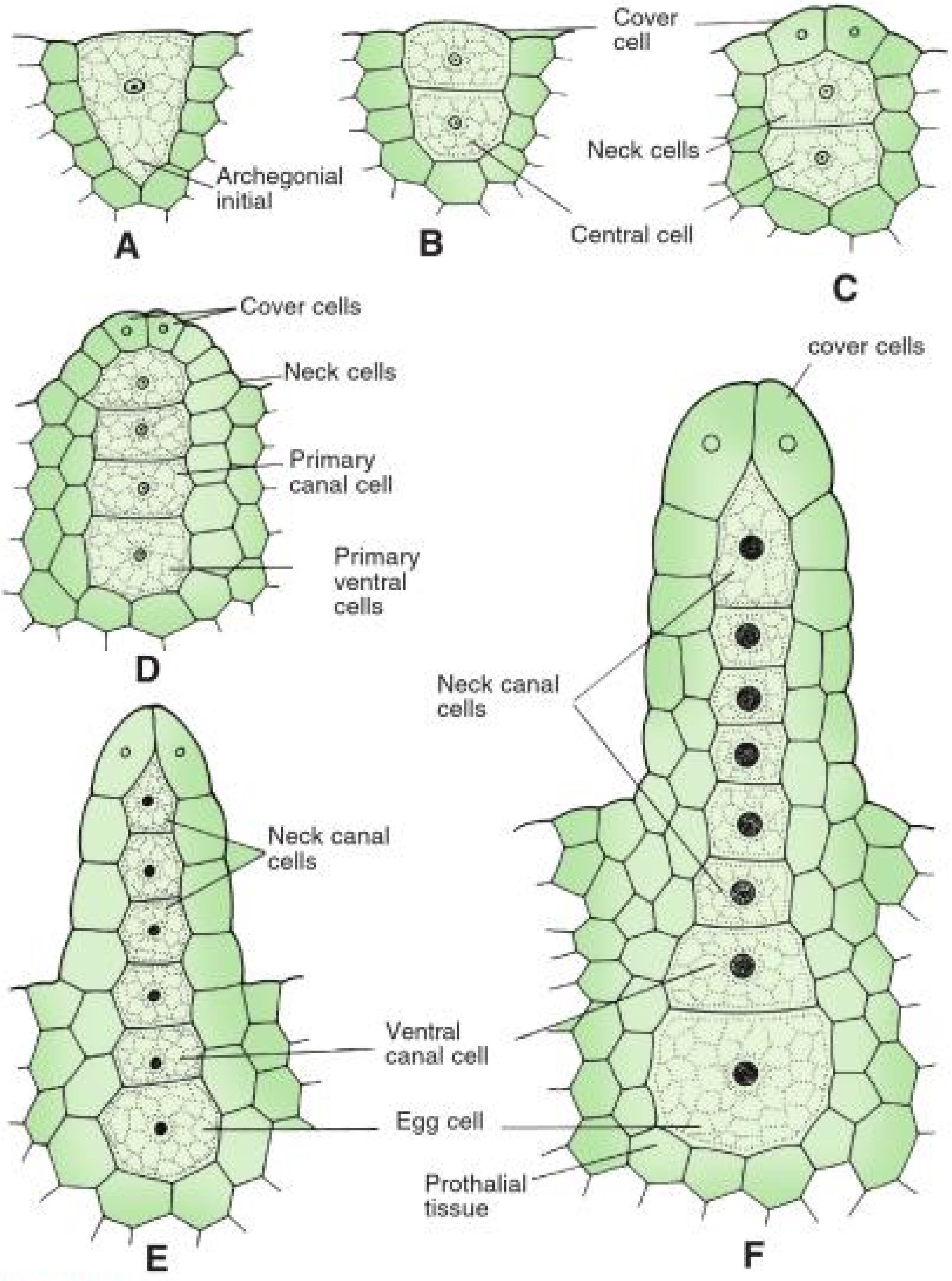

Cover cell
Archegonial initial
Neck cells
Central cell
A
B
C
Cover cells
Neck cells
Primary canal cell
Primary ventral cells
D
cover cells
Neck canal cells
Neck canal cells
Ventral canal cell
Egg cell
Prothalial tissue
E
F

Fig. 4.19 (a). *Lycopodium selago (A-F).* Various stages in the development of archegonium.

THE EMBRYO

The embryology in all the species of ***Lycopodium*** is **endoscopic** (***i.e.***, the shoot apex is directed away from the archegonial neck). The earlier stages of development, in all the species, are similar. The nucleus of the oospore divides into two daughter nuclei that are separated by a transverse wall (Fig. 4.20, A). This first division of the oospore determines the polarity of the embryo. It results in the formation of an **epibasal** and a **hypobasal cell**. The cell next to the archegonial neck is **epibasal** and away from it is the **hypobasal cell**. The epibasal cell enlarges to function as the suspensor. Rarely it may divide once or twice. The **hypobasal cell** or the **embryonal cell** gives rise to the embryo and divides by transverse and longitudinal walls to form two quadrants (Fig. 4.20, C). The

hypobasal quadrant which is next to the suspensor cell divides further and gives rise to the foot (Fig. 4.21, A). The **epibasal quadrant** forms the shoot and the primary root (Fig. 4.21, A). Further growth of the embryo pushes it deep into the tissue of the prothallus (Fig. 4.21, C) and away from the archegonial neck. Later stages in embryology of different species are variable and shall be considered under three headings:—

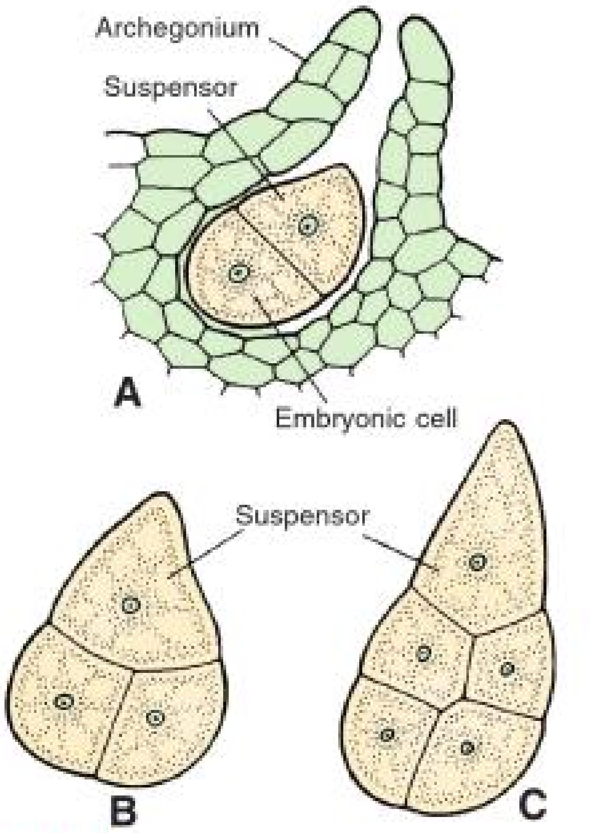


Fig. 4.20. *Lycopodium clavatum.* Early stages of embryo development.

LYCOPODIUM SELAGO AND L. PHLEGMARIA

In these species the foot is quite prominent and develops from the hypobasal quadrants of the octant stage. The epibasal quadrants form an apical meristem by repeated longitudinal and transverse divisions. In ***L. phlegmaria*** (Fig. 4.21, A–C) the foot is massive as compared to ***L. selago***. The foot and the apical meristem divide in different planes, but the divisions are quite regular. The embryo is deeply embedded in the prothallus tissue (Fig. 4.21) and has large cells in foot region. Later divisions result in a curved embryo that bursts through the prothallus tissue in an upward direction. Its apex is the shoot apex made up of a row of meristematic cells. Root differentaties laterally above the foot in the leaf quadrant. Leaf primordia and stem primordia differentiate from the shoot meristem. The leaf primordia arise in a spiral sequence. The shoot and the root regions are traversed by a distinct procambial strand that later matures into the vasculature of the root and the shoot. Further development leads to the emergence of first stem that grows erect and carries the cotyledons above. Later other leaves appear. The root grows down but is sort-lived and is soon replaced by adventitious roots.

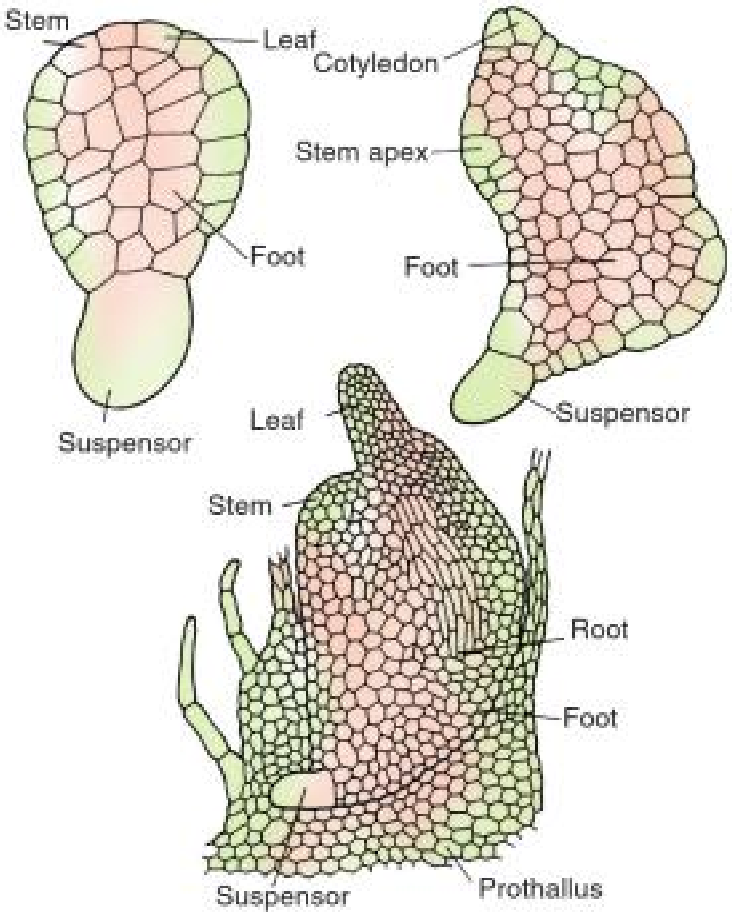


Fig. 4.21 (A-C). *Lycopodium phelgmaria.* Later stages of embryo development. (After Treub)

L. CLAVATUM AND L. ANNOTINUM

In these species the foot is massive and haustorial and the growth of the apical region of the embryo is comparatively very slow and the first two leaves are opposite and not spiral as in ***L. selago***. They develop late and are scale-like. The procambial strands also develop late. In these creeping species first stem is soon replaced by the horizontal stem which arises from the base of the former and bears colourless scale leaves that are devoid of midrib and vascular supply. The development is very slow and this young sporophyte depends for years together on the subterranean, gametophyte for nutrition. It takes many years for it to come above ground and become independent.

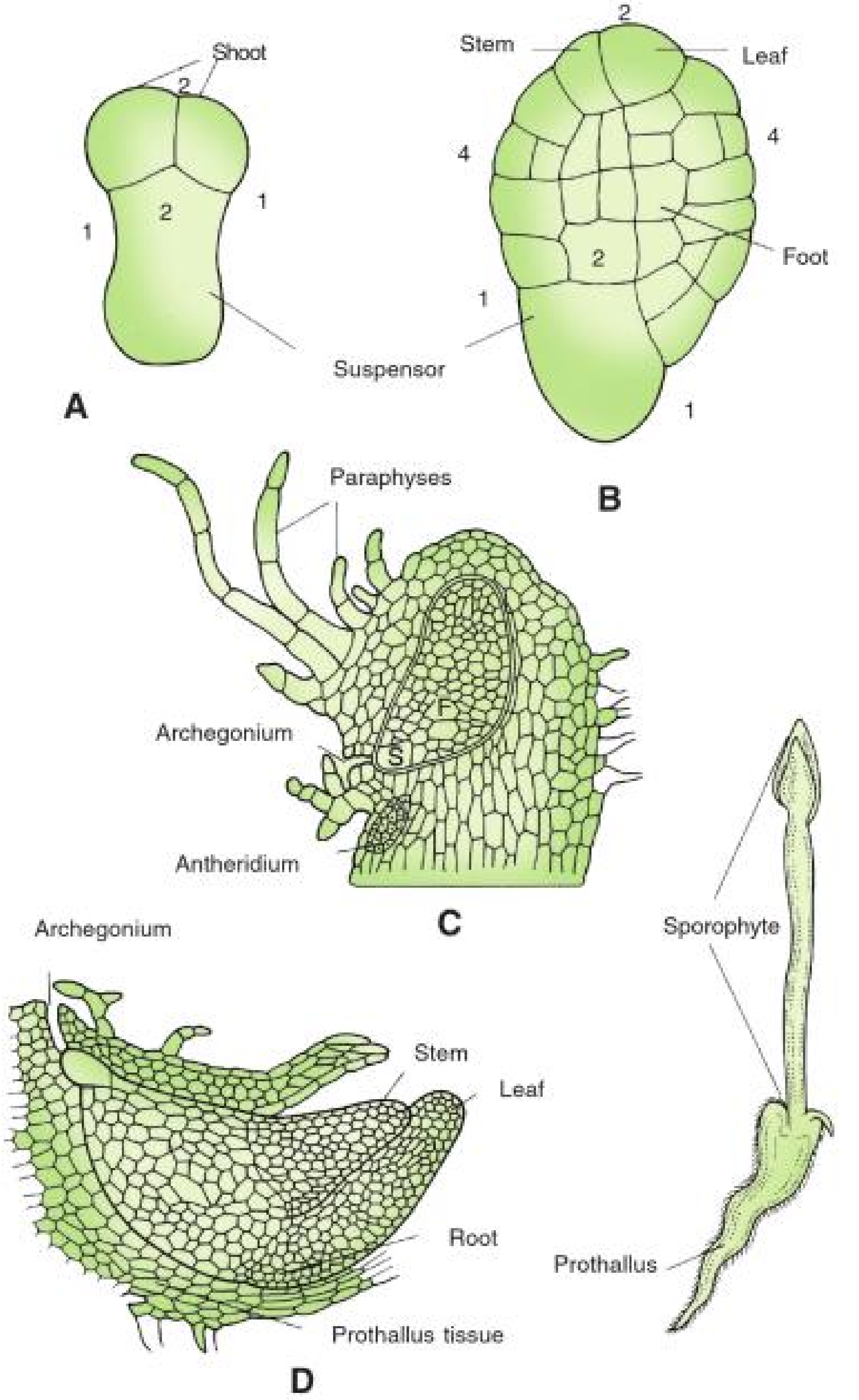

Shoot
2
1
2
1
Suspensor
A
2
Stem
Leaf
4
4
Foot
2
1
1
B
Paraphyses
Archegonium
F
S
Antheridium
C
Archegonium
Stem
Leaf
Root
Prothallus tissue
D
Sporophyte
Prothallus

Fig. 4.22 (A-E). *Lycopodium selago.* **A.** Young embryo as seen in L.S. The wall 1-1 has divided it into suspensor segment and shoot segment; **B.** L.S. through older embryo showing suspensor, foot, stem and leaf segments. Positions of walls 1-1, 2-2 and 4-4 are clear; **C.** Later stage of embryo still enclosed the prothallus tissue; **D.** Mature embryo breaking through the prothallus tissue, S = suspensor; F = foot; **E.** A young sporophyte attached to prothallus. (After Bruchmann).

L. CERNUUM AND L. INUNDATUM

These species are characterised by the development of a tuberous mass of cells called the **protocorm** from the epibasal quadrant (Fig. 4.23). It is made up of undifferentiated mass of parenchymatous cells. It bears numerous rhizoidal hair that attach it to the soil. The cells at the base contain a symbiotic fungus. A conical outgrowth develops on the upper surface of the protocorm. It soon grows into a cylindrical green leaf or **protophyll**. This is followed by the formation of an indefinite number of **protophylls**, without any regular arrangement (Fig. 4.23, B, C). Both the protocorm and the protophylls lack a vascular strand. They are green and the protophylls possess stomata. The protocorm with its protophylls soon loses contact with the prothallus. It is at a later stage that the **shoot apex** can be recognised at the distal end of the protocorm. The shoot apex develops close to the last formed protophylls. It soon becomes prominent and bears young leaves in a normal phyllotactic sequence. At a later stage a primary root also arises and penetrates the soil. It is exogenous in origin. Procambial strands also develop in the young sporophyte and later mature into vascular tissue.

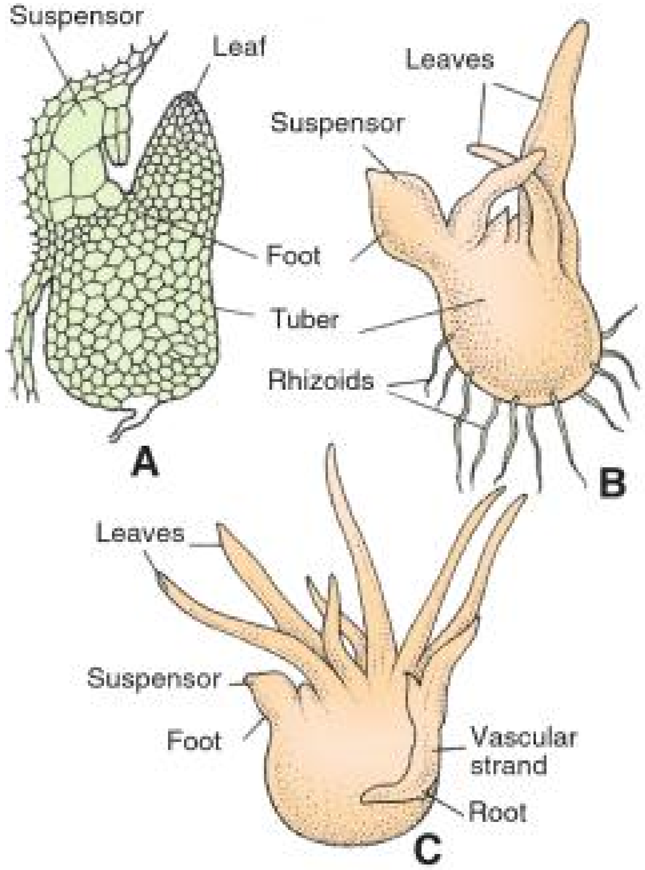


Fig. 4.23 (A-C). ***Lycopodium cernuum.*** **A.** Young embryo has grown through the prothallus; **B.** Embryo showing differentiation into leaf, foot and tuber, Rhizoids have also developed from the tuber; **C.** An embryo with three leaves.

Morphology of the Protocorm

Treub regarded protocorm as a primitive structure that has been retained as an ancestral feature by some contemporary species. He visualised that it must have been present in the ancestral vascular plants. Treub's view has not received popularity and is now regarded as of historical importance only.

Bower (1907, 1935) regarded it as an 'Opportunist growth' that developed in certain species of ***Lycopodium*** as a response to the prevailing environmental conditions. He attaches only an ecological importance to this structure. It serves only to establish the young sporophytes to soil and has no phylogenetic importance.

Browne (1913) regarded the protocorm as a modified and a reduced stem.

Holloway regarded the protocorm as a specialised structure that helps the young sporophyte to perennate over dry season and that it has no phylogenetic significance.

Wardlaw (1935) regarded the protocorm as a modified shoot. He is of the opinion that its regular appearance in certain species of ***Lycopodium*** is not due to any environmental effect but to certain genetic factors that must be involved in its persistence in these species. He attributed the development of protocorm to certain metabolic conditions of the prothallus and young sporophyte. According to him, carbohydrate and nitrogen ratio (C/N) is responsible for the development of localised swellings in the embryo. In case the embryo received a balanced nutrition and C/N ratio is normal the embryo produces no swellings and produces normal enlongating leafy shoot. In case the embryo receives unbalanced nutrition and C/N ratio is high the organisation of the young shoot apex is delayed and protocormous outgrowths develop. Wardlaw states that in ***L. cernuum*** and ***L. laterale*** (protocormous species) the genes which determine protein synthesis at the shoot apex are ineffective in the beginning. This leads to the delay in the development of shoot apex and aids in the formation of a new structure called the **protocorm**. Later the green **protophylls** and **protocorm** as a result of their photosynthetic activity produce certain essential metabolic products that lead to the growth of the shoot. The ineffective gene is thus switched on to activity.

Deviations from Normal Life Cycle

Occurrence of the phenomenon of apospory and apogamy in ***Lycopodium*** has not so far been reported in nature. Recently Freeberg (1957) was able to induce apogamy in ***L. complanatum***, ***L. cernuum*** and ***L. selago***. He was able to grow these species under cultural conditions by germinating their spore on culture media. He got full-fledged gametophytes that bore sex organs and produced after normal fertilisation, embryo and young sporophytes. During his experiments he found that under conditions unfavourable for fertilization (absence of water) the gametophytic tissue produces complete sporophytic plants apogamously. The young sporophytes arise apogamously from the tips of the branches of prothalli. Gametophytic tissue was also induced to produce a single leaf. Such apogamously produced sporophytes were also observed, in rare cases, to produce from the stem a gametophyte like outgrowth. Only one such case of formation of aposporous gametophyte was observed by Freeberg (1954). De Maggio (1964) induced apogamy in the gametophytes of ***L. obscurum*** by supplying coconut milk or sucrose or both to the nutrient medium. He was able to induce the formation of root buds in the gametophytic callus of this species.

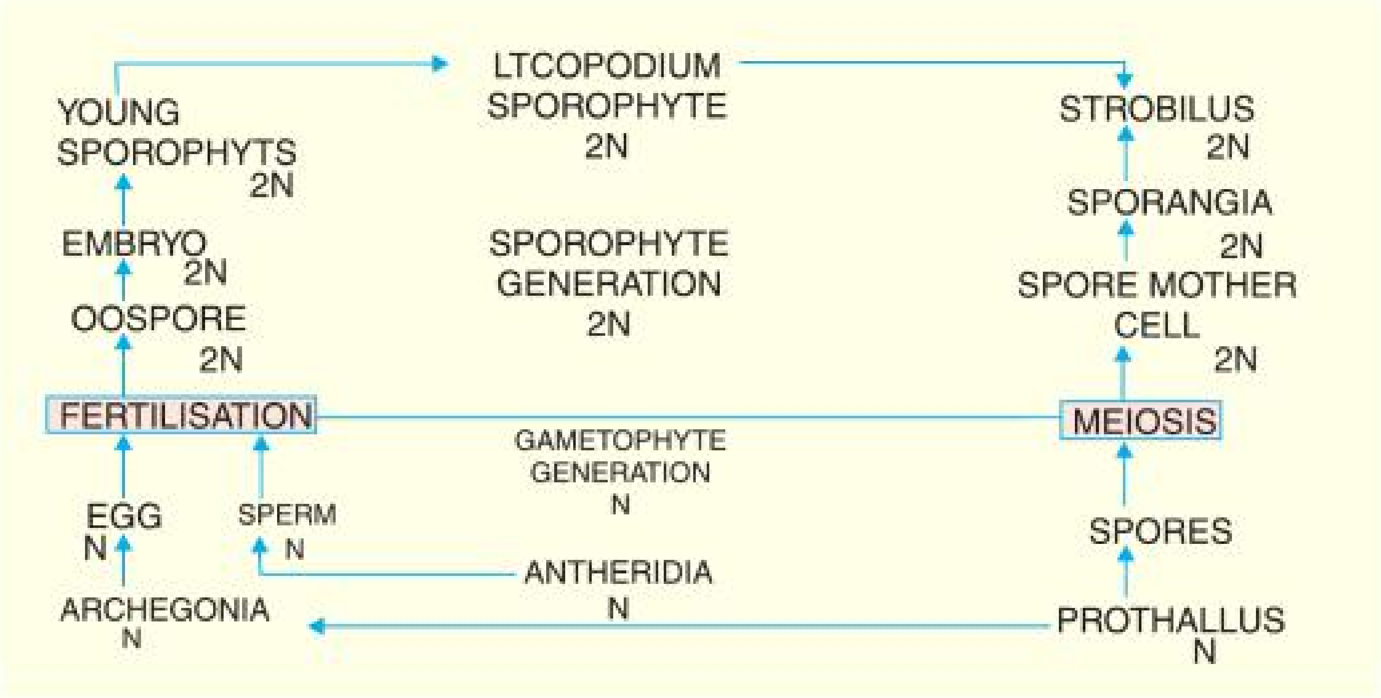


Fig. 4.24 A. Graphic representation of life cycle of *Lycopodium.*

Economic Importance

The spores of ***Lycopodium inundatum*** and some other species yield 50% fixed oils. They are much used as cover for pills, as a diluent for insufflations, and as a dusting powder for abraded surfaces. In industry they are used for making pattern molds ; because of their inflammability they are used in flares, fireworks and tracer bullets. Some species have a medicinal value also. ***Lycopodium*** is widely used in the homoeopathic system of medicine.

Chromosome Numbers

Cytology of a number of species has been worked out (Dunlop 1949; Manton, 1950; Mehra and Verma 1957; Ninan, 1958) and the haploid number of chromosomes in the various species has been confirmed to vary between ***n*** =14 to ***n*** = 136. Dunlop (1949) and Manton (1950) reported 2***n*** = 260 in ***L. selago***. They found that in this species during meiosis there are a number of unpaired chromosomes that show this species to be a hybrid. Such observations go against the supposition that ***L. selago*** is an intermediate type.

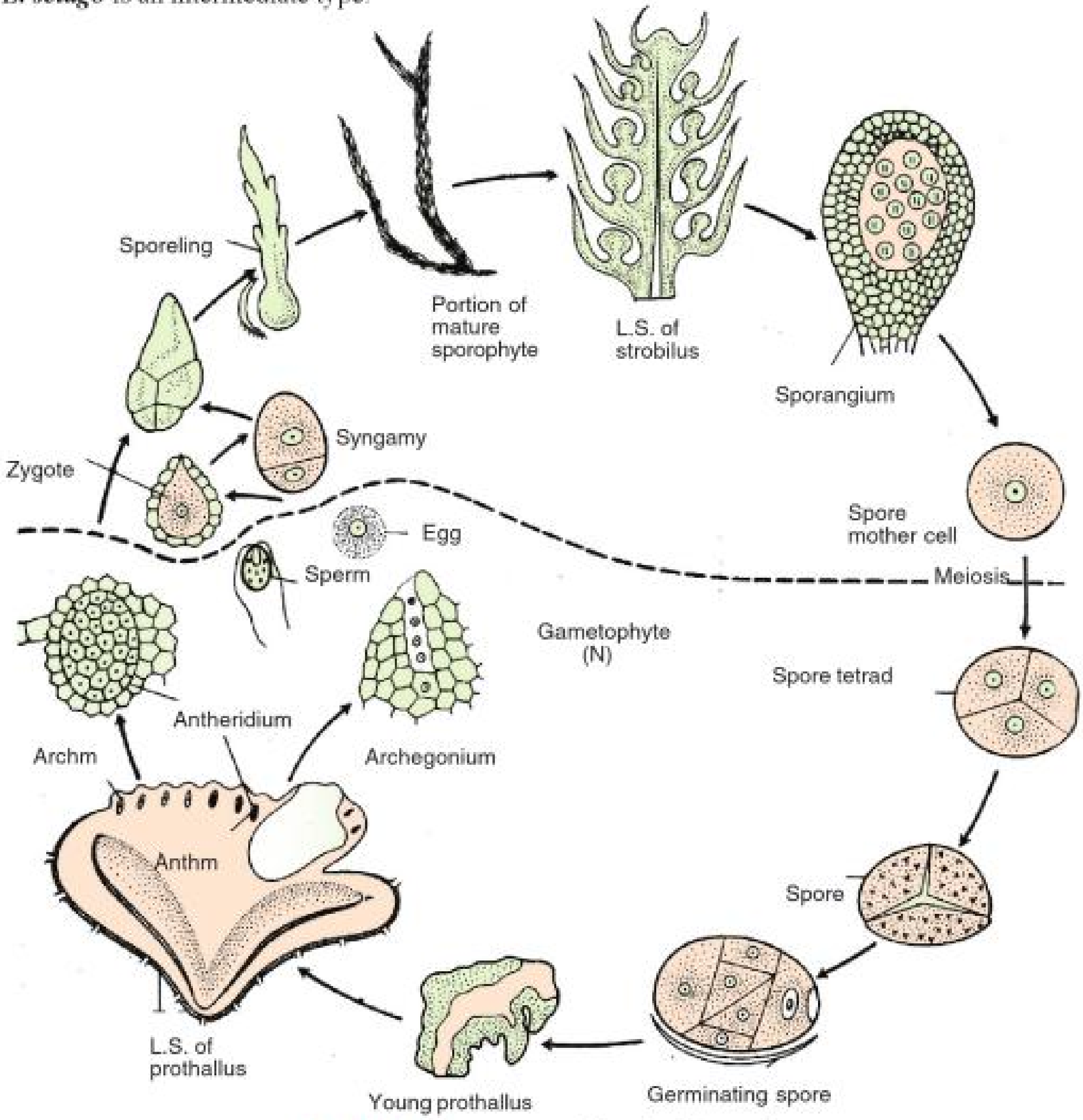

Sporeling
Portion of mature sporophyte
L.S. of strobilus
Sporangium
Syngamy
Zygote
Egg
Spore mother cell
Sperm
Meiosis
Gametophyte (N)
Spore tetrad
Antheridium
Archm
Archegonium
Anthm
Spore
L.S. of prothallus
Young prothallus
Germinating spore

Fig. 4.24 B. Diagrammatic life cycle of *Lycopodium*

Taxonomic Position

Division : ***Lycophyta***
Class : ***Eligulopsida***
Order : ***Lycopodiales***
Family : ***Lycopodiaceae***
Genus : ***Lycopodium***

PHYLLOGLOSSUM Kunze

It is the second monotypic genus of the lycopodiaceae and is represented by ***Phylloglossum drummondii***. In its habit it resembles the young protocormous sporophytes of ***Lycopodium cernuum***

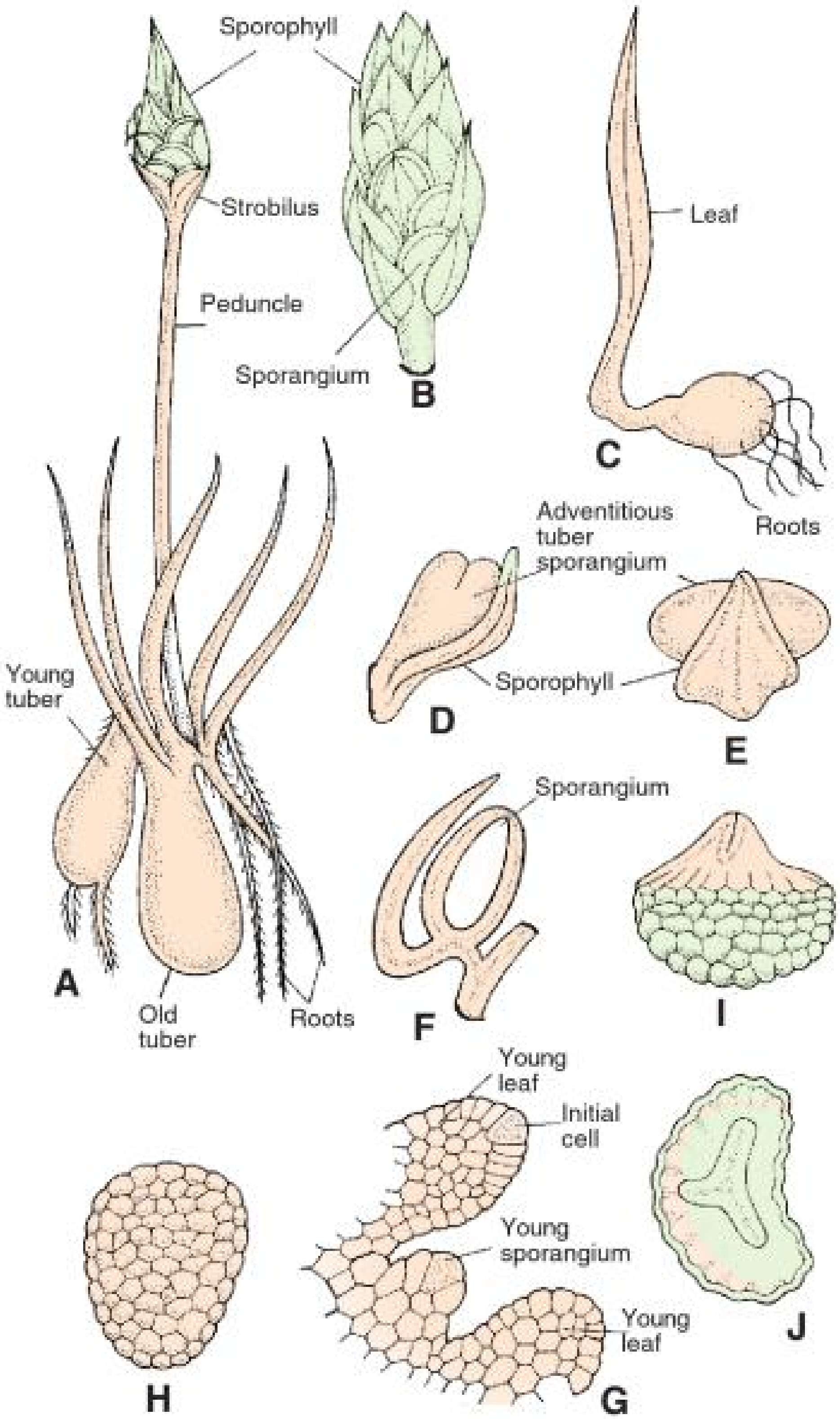

Sporophyll
Strobilus
Peduncle
Sporangium
B
Leaf
C
Roots
Adventitious
tuber
sporangium
Sporophyll
D
E
Young
tuber
Sporangium
A
Old
tuber
Roots
F
I
Young
leaf
Initial
cell
Young
sporangium
Young
leaf
J
H
G

Fig. 4.25 (A–J) ***Phylloglossum drummondii.*** **A.** a complete plant showing habit. Note the young and old tuber and position of leaves and roots; **B.** Portion of spike enlarged; **C.** Isolated leaf with adventitious tuber; **D.** Lateral view of the sporophyll with an axillary sporangium; **E.** Sporophyll and sporangium as seen from distal end. The sporangium is foliar; **F.** Radial section of the sporophyll bearing a foliar sporangium. The sporangium has dehisced; **G.** L.S. Young strobilus; **H.** Spore as viewed from below; **I.** Spore as seen from side; **J.** Spore as seen from above. (All after Bertrand)

and ***L. laterale***. It has a restricted distribution and occurs only in New Zealand, Tasmania and Southern and Western Australia. The sporophytes of this species (Fig. 4.25, A) make their appearance above ground only during winter and reach a maximum height of four centimetres. This interesting genus has been studied in detail by Bower (1885) and Bertrand (1885, 1886).

The underground portion of the plant is a small ovoid and fleshy tuber or the 'protocorm' (Fig. 4.25, A). Usually there are two tubers, one of the preceding year that shows signs of exhaustion, and the other younger one that is in the course of development and stores food (Fig. 4.25, A) for the succeeding year. Both the tubers are borne on distinct stalks. The young tuber arises from the apex of the older one. The roots arise exogenously from the crown of the tuber and may vary in number from one to three. The aerial parts of the plant are three to twenty green leaves and an erect green peduncle bearing a terminal strobilus (Fig. 4.25, A). The leaves are cylindrical and arise in a whorl from the apex of the tuber (Fig. 4.25, A). The leaves have no definite position or phyllotaxy. They surround a small and simple axis which later grows into an erect peduncle bearing terminal strobilus. In rare cases the strobilus may branch dichotomously.

During hot summer months the aerial green parts of the plant die and the only part that survives is the subterranean tuber. The tuber with its stored food lies dormant until the next year. During winter it resumes activity and bears a secondary tuber and a fresh crown of green leaves. The secondary or sometimes even tertiary tubers develop from the apices of lateral stem like branches that grow out and downwards.

The sporophyte reproduces vegetatively by forming secondary tubers that strike their own adventitious roots and on separation from the parent tuber develop into new individual plants. Isolated leaves (Fig. 4.25, C) have also been observed to develop tubers (Osborn, 1919). Osborn has described the regeneration of new tubers on detached leaves. When such leaves are laid down on moist soil, one or several epidermal cells near the proximal end on the abaxial surface proliferate to form a primary cell mass (fig. 4.27). From a growing point differentiated on this cell mass a tuber develops which resembles that formed by the normal plant. The results obtained were applied to the problems presented by the tuber and the protocorm. Osborn concluded that the primary cell mass is homologous to the protocorm and that the tuber is an entirely different structure of great biological value to the plant, but having little morphological significance.

Anatomy (Fig. 4.26, A-C)

Sections of the tuber and the peduncle through various levels reveal a striking variation in stelar system. In the lower storage region of the tuber there are no traces of vasculature. Near the apex of the tuber the stele is **amphiphloic siphonostele** (Fig. 4.26, C). It is broken by the departure of branch trace to the stalk of the new tuber. The branch trace leaves a gap called the branch gap. Above this region is the base of peduncle or the stem. A section through the basal region of the peduncle shows an unbroken (Fig. 4.26, B) **amphiphloic siphonostele**. A little above this the stele becomes simple **ectophloic siphonostele** with mesarch xylem. In the terminal region and in the strobilus the peduncle shows a ring of discrete strands ***i.e.*** it is a dictyostele (Fig. 4.26, A).

In less developed sporophytes a section through the base of the peduncle shows a protostele with mesarch xylem. So sections cut at the various levels of the axis of this small plant show all important types of steles ***i.e.*** **protostele**, the **siphonostele** (both ectophloic and amphiphloic) and the **dictyostele**. Presence of all these types of steles within a short height of four centimetres is suggestive of the fact that all these types are modifications of one fundamental type of stele, the **protostele.**

The anatomy of the root is very simple. A transverse section reveals a monarch or a diarch stele surrounded by the cortex.

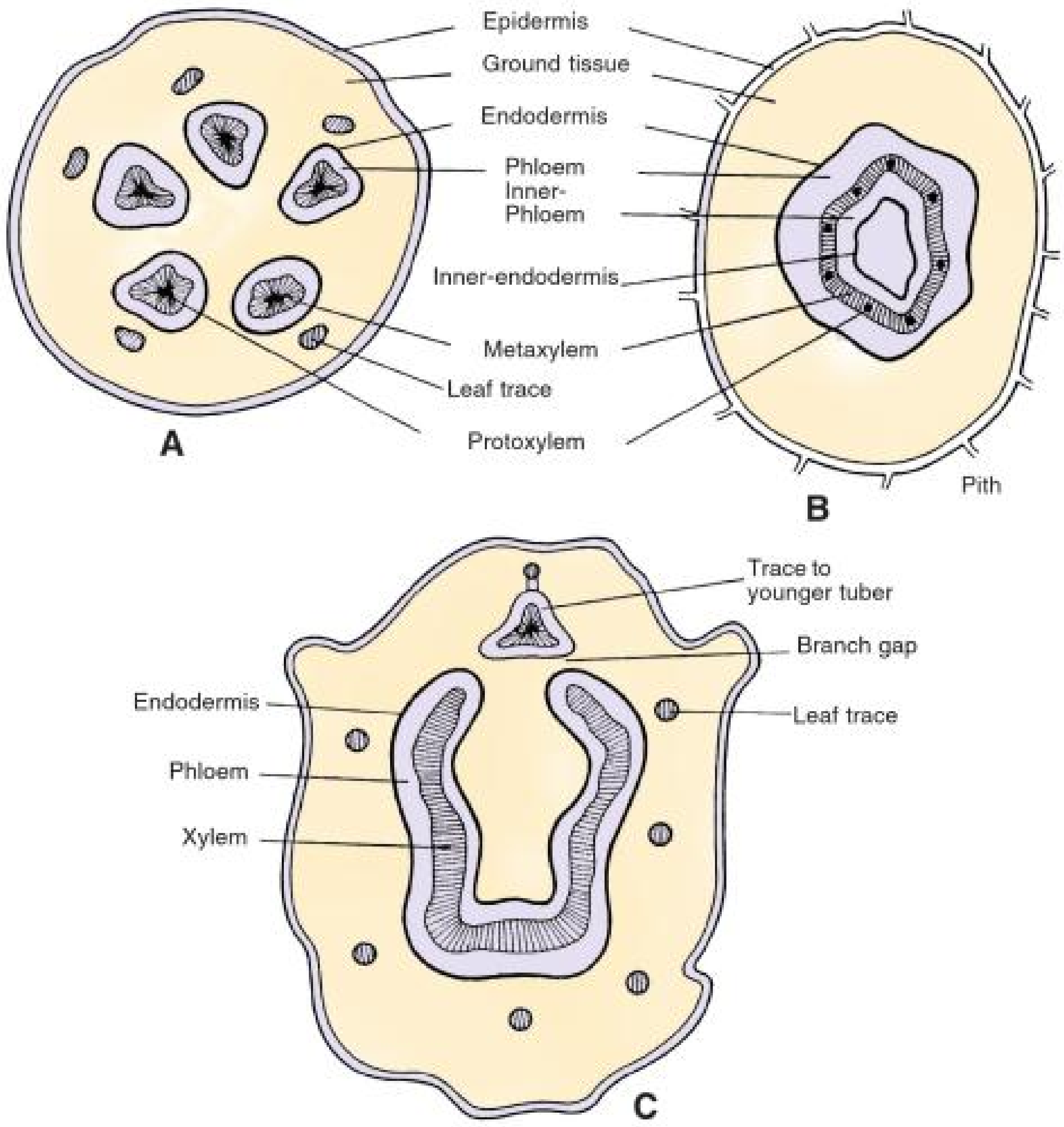

Epidermis
Ground tissue
Endodermis
Phloem
Inner-Phloem
Inner-endodermis
Metaxylem
Leaf trace
Protoxylem
Pith
A
B
Trace to younger tuber
Branch gap
Endodermis
Leaf trace
Phloem
Xylem
C

Fig. 4.26 (A–C) Anatomy of the tuber and penduncle of ***Phylloglosum drummondii.*** **A.**T.S. Through upper part of the peduncle showing dictyostelic condition; **B.** T.S. Through middle portion showing amphiploic siphonostele; **C.**T.S. Through top of the tuber showing siphonostele with a branch gap.

A transverse section of the cylindrical leaf (Fig. 4.27) also reveals a single central vascular strand surrounded by an undifferentiated mesophyll which in turn is enveloped by a distinct layer of epidermis.

Organization of the Strobilus

The strobilus is terminal in position (Fig. 4.25, A, B) and is quite distinct. It has a central axis with sporophylls arranged without any definite pattern. They appear to arise in whorls in the lower part of the strobilus. The sporophylls are small and scale like and yellowish in colour. They have a broad base with narrow and pointed (Fig. 4.25, D–F) apex and may be sessile or subsessile. The sporophylls in the middle of the cone appear to be subsessile and those at the base sessile. The sporangia arising in the axils of lower sessile sporophylls are shortly stalked and cauline in origin.

The middle subsessile sporophylls bear sessile sporangia that are foliar in origin. Each sporangium is reniform in shape and yellow in colour. It has a two or three layered thick wall. The innermost wall is the **tapetum**. It has been observed to persist up to the formation of **spore mother cells**. The sporangia open by a median slit extending from the top to base. The two valves open and permit the spores to escape. The spores are arranged in tetrahedral tetrads. Each mature spore has a tetrahedral shape with sculptured exine and a distinct triradiate mark (Fig. 4.25, H., J). They are yellow in colour.

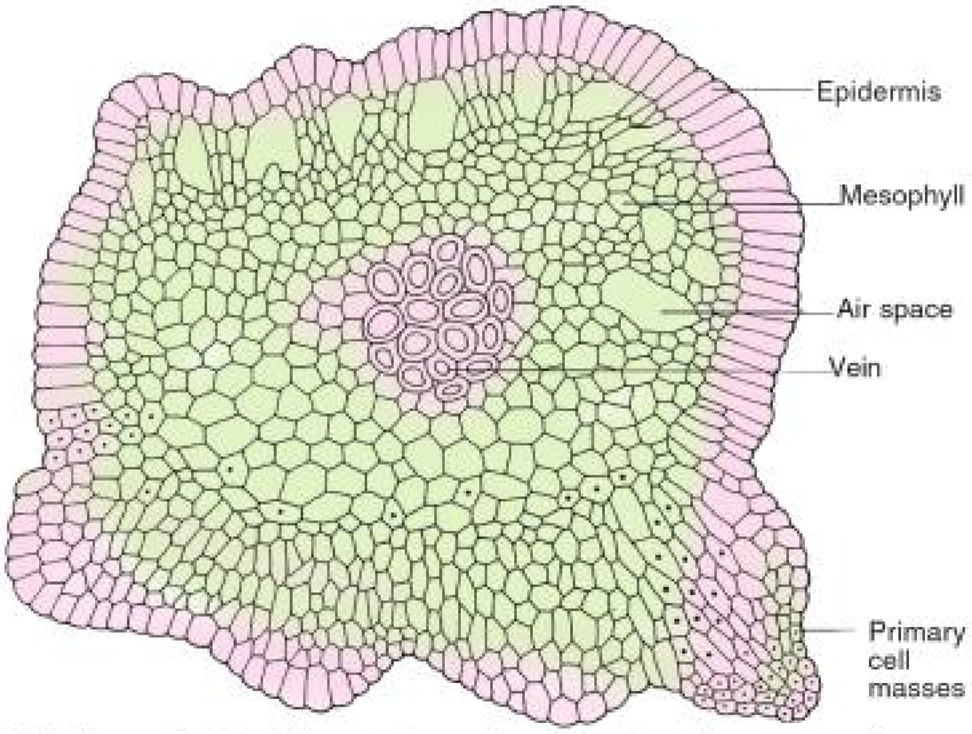


Fig. 4.27. ***Phylloglossum***. T.S. Leaf showing internal structure. Note the primary cell masses.

Gametophyte (Fig. 4.28)

Thomas (1901) described the gametophytes of **Phylloglossum**. They resemble those of ***L. cernuum*** and have abundant chlorophyll. They are about two to four millimetres long and have a lower short, thick and cylindrical portion called the basal zone. The upper crown is irregular or lobed (generative zone). The lower end of the gametophyte is conical (Fig. 4.28) and colourless. It is infected with endophytic fungus and is subterranean. The crown is above ground and green. The antheridia and archegonia arise in crown and have same structure as ***Lycopodium***. Thomas did not study the spermatozoids.

Bertrand stated that M. L. Crie has described the germination of spores. According to Crie, the spores germinate readily and produce a colourless gametophyte. He has also described the spermatozoids to be bicilliate. Crie's account is different from Thomas.

Embryo

The embryo development has not been studied in detail. Thomas (1901) and Sampson (1916) have given brief descriptions of the embryo. They describe it to be similar to ***L. cernuum***. The embryo is attached laterly to the gametophyte. It has a prominent foot which attaches it to the gametophyte. The leaf and the stem apex break through the prothallial tissue and come out laterally. At this stage the embryo appears cylindrical. The lower part swells up, becomes fleshy and forms the tuber, the upper end grows into the first green and cylindrical leaf. The leaf has a vascular strand. The tuber has often been regarded as a ***protocorm***. Eames (1986) is not in favour of this view. He regards it a true tuber of the first season because it bears a true leaf that is traversed by a distinct vascular strand. The tuber bears no root for the first season and has only one leaf. Roots appear later and so do other leaves.

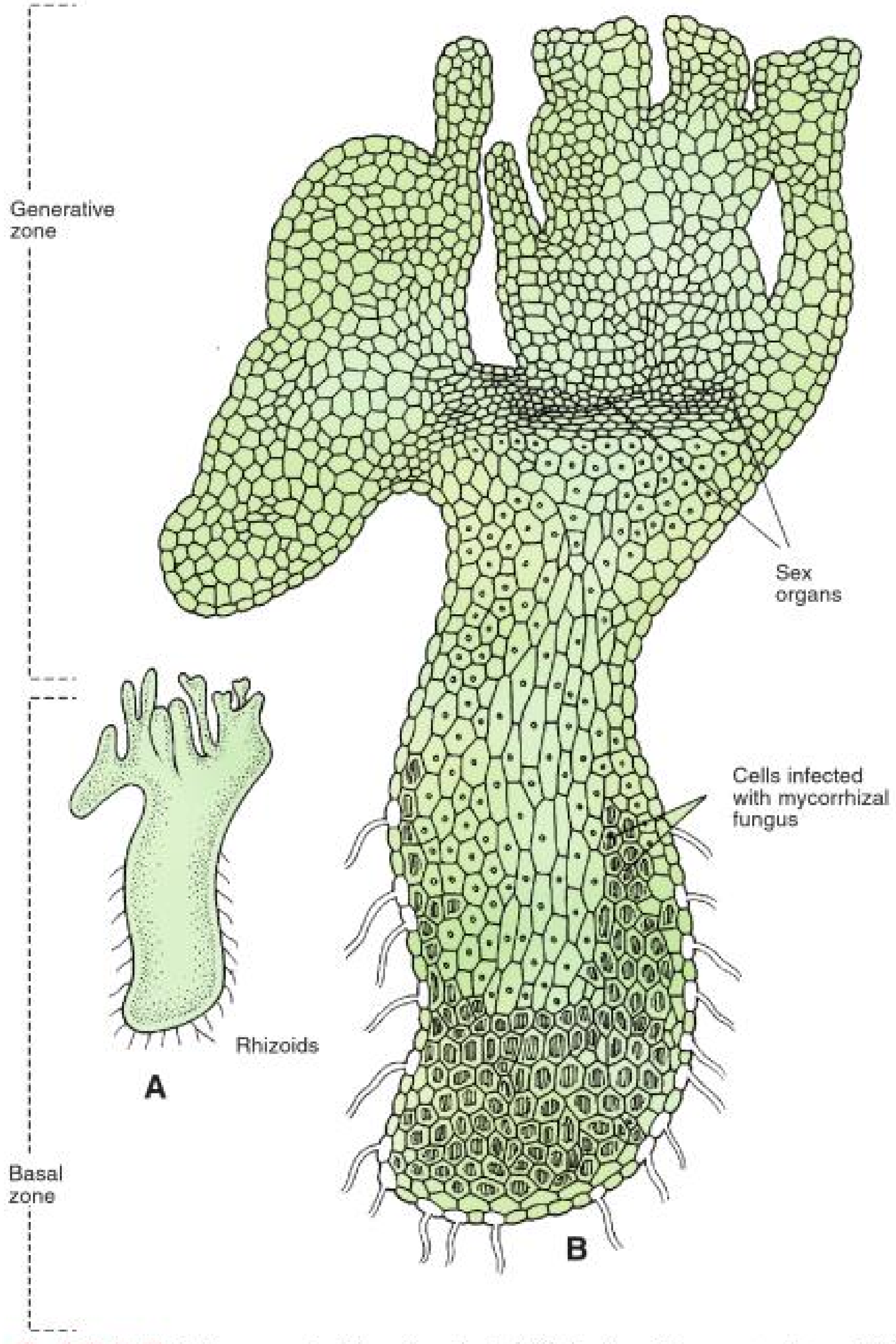

Generative zone
Sex organs
Cells infected with mycorrhizal fungus
Rhizoids
A
Basal zone
B

Fig. 4.28 (A-B). A diagrammatic (A) and hypohetical (B) drawing of the gametophyte of *P. drummondii*

Taxonomic Position

Division : ***Lycophyta***
Class : ***Eligulopsida***
Order : ***Lycopodiales***
Family : ***Lycopodiaceae***
Genus : ***Phylloglossum***

QUESTIONS

ESSAY TYPE

1. How many types of gametophytes are found in ***Lycopodium***? Why it is always difficult to collect such prothalli in nature? Illustrate your answer with suitable diagrams.
2. (*a*) Discuss the structure and nature of Protocorm.
   (*b*) Describe structure of nature gametophytes of ***Lycopodium***.
3. Write a comparative account of different types of gametophytes met in ***Lycopodium***. Which of them is regarded an primitive and why?
4. With the help of suitable sketches describe the stem anatomy of ***Lycopodium*** and mention the different types of steles found in it.
   (Kanpur, 2002; Lucknow, 2001)
5. By means of labelled diagrams only illustrate the life cycle of ***Lycopodium***.
6. Give a comparative account of the gametophytes of ***Lycopodium*** and ***Selaginella***.
7. Define the term stele. How many types of steles are found in ***Lycopodium***? Illustrate your answer with suitable diagrams.
8. With the help of labelled diagrams, illustrate the lifecycle of ***Lycopodium*** and point out its important features.
9. Give an illustrated comparative account of gametophytes, of ***Psilotum***, ***Lycopodium*** and ***Ophioglossum***.
10. Describe the spore producing organs (strobili) of ***Lycopodium*** and ***Selaginella***.
11. How does eusporangiate type of sporangium development differ from that of Leptosporangiate type? Describe the structure and development of sporangium in ***Lycopodium***.
12. Describe the similarities and dissimilarities of the gametophytes of ***Lycopodium*** and ***Selaginella***.
13. Give a comparative account of spore bearing organs of ***Lycopodium***, ***Selaginella*** and ***Equisetum***. Support your answer with labelled sketches. **(Lucknow, 2001)**
14. Give a brief account of the internal structure of the stem of ***Lycopodium***.
    (Lucknow, 2001)
15. Describe the stelar types in the species of ***Lycopodium*** with illustrations. **(Kerala, 2000)**
16. Describe briefly the following
    (*a*) Different types of protostele in the stem of ***Lycopodium***.
    (*b*) Stelar system in ***Lycopodium***.
    (*c*) Any two types of gametophytes of ***Lycopodium***.
    (*d*) Mature gametophyte of ***Lycopodium cernuum***.
    (*e*) Three types of gametophytes of ***Lycopodium***.
    (*f*) Gametophyte of ***Lycopodium***.
17. Describe the stelar types (organisation) in the species of ***Lycopodium*** with illustrations.
    (Kerala, 2001; Lucknow, 2002)
18. Give an account of different types of gametophytes of ***Lycopodium*** and comment on their association with endophitic fungi.
19. Describe the sporophytic generation, distribution and external feature and internal anatomy of ***Lycopodium***.
20. (*a*) Give an account of various types of steles found in ***Lycopodium***.
    (*b*) Describe the term stele. How many types of steles are found in ***Lycopodium*** ? Illustrate your answer with suitable diagrams.
    (Allahabad, 2004)
21. Describe the structure of spores in ***Lycopodium***. How does it germinate and form the prothallus? Illustrate your answer with diagrams.
22. Describe the structure and development of sex organs with the help of diagrams.
23. Where is ***Phylloglossum*** found? Give a detailed account of the structure and anatomy of the adult plant.
24. By means of labelled diagrams, describe the anatomy of the tuber, peduncle and leaf of ***Phylloglossum***.
25. Describe the gametophyte and embryo of ***Phylloglossum***.

SHORT ANSWER TYPE

26. **Answer the following:**
    (*i*) Name a pteridophyte which has mycorrhiza in its gametophyte.

(*ii*) Name a pteridophyte in which vegetative reproduction takes place by gemmae.

(*iii*) Which pteridophyte is called "club moss". **(Kanpur, M.Sc. 2000)**

(*iv*) Name a homosporous pteridophyte.

(*v*) Name a pteridophyte which has plectostele. **(Kanpur, 2000)**

(*vi*) (*a*) Where is protocorm formed?

(*b*) What is protocorm?

(*vii*) Name the pteridophyte having different types of steles.

(*viii*) From which place will you collect ***Lycopodium***. **(Kanpur, 2000)**

(*ix*) Where does ***Lycopodium phlegmaria*** grow in nature?

(*x*) Name a pteridophyte whose spores were used as explosive during the Ist World War.

(*xi*) Mention the names of two subgenera of ***Lycopodium***.

(*xii*) Why is it always difficult to discover and collect the prothalli of ***Lycopodium*** in nature?

(*xiii*) How can you explain the occurrence of ***Selago*** condition as ***Lycopodium***?

(*xiv*) Name a pteridophyte and its species which shows the presence of protocorm in it. **(Allahabad, 2001)**

(*xv*) Write botanical name of club moss.

(*xvi*) Give the function of protocorm.

(*xvii*) What is selego condition? **(Poorvanchal, 2000)**

(*xviii*) Is protocorm a sporophyte or gametophyte?

(*xix*) Name an epiphytic species of ***Lycopodium***. **(Lucknow, 2001)**

(*xx*) What are the types of steles in ***Lycopodium***.

(*xxi*) Mention the stelar types in ***Lycopodium***.

(*xxii*) What is the name of common species of ***Phylloglossum***.

(*xxiii*) How does ***Phylloglossum*** reproduce vegetatively?

(*xxiv*) What is the shape of spore of ***Phylloglossum***?

(*xxv*) Name a pteridophyte which has primary cell masses in the leaf.

(*xxvi*) Which chemical substance is evolved during the disintegration of neck canal cells and ventral canal cells in ***Lycopodium*** ? **(Allahabad, 2003)**

27. Write short notes on

(*i*) Prothallus of ***Lycopodium*** **(Kanpur, 2000; Awadh, 2000)**

(*ii*) Protostele. **(Meerut, 2000)**

(*iii*) Economic importance of ***Lycopodium***.

(*iv*) Gametophytes of ***Lycopodium clavatum***.

(*v*) Protocorm **(Kumaon, 2000; Bangalore, 2001)**

(*vi*) Types of steles in stems of ***Lycopodium*** species.

(*vii*) Steles in ***Lycopodium***. **(Devi Ahilya, 2001)**

(*viii*) Morphology of Protocorm.

(*ix*) Spore producing organs of ***Lycopodium***.

(*x*) Gametophyte of ***L. cernuum***. **(Poorvanchal, 2000)**

(*xi*) Stelar organisation in the stem of ***Lycopodium***.

(*xii*) ***Lycopodium*** strobilus. **(Bangalore, 2001; Meerut, 2000)**

(*xiii*) Different types of gametophytes of ***Lycopodium***. **(Devi Ahilya, 2001)**

(*xiv*) Stem anatomy of ***Lycopodium***.

(*xv*) Vegetative reproduction in ***Lycopodium***.

28. Differentiate between.

(*a*) Cones of ***Lycopodium*** and ***Selaginella***.

(*b*) Sperms of ***Lycopodium*** and ***Equisetum***.

(*c*) Root and Stem of ***Lycopodium***.

(*d*) T. S. Stems of ***L. cernuum*** and ***L. clavatum***.

(*e*) Reproductive bodies of ***Lycopodium*** and ***Equisetum***.

(*f*) Gametophyte of ***Lycopodium cernuum*** and ***Equisetum debile***.

(*g*) Leaves of ***Lycopodium*** and ***Selaginella***.

(*h*) Prothallus of ***Lycopodium*** and ***Selaginella***. **(Lucknow, 2000)**

(*i*) ***Phylloglossum*** and ***Lycopodium***.

(*j*) Gametophytes of ***Lycopodium*** and ***Phylloglossum***.

29. Draw labelled diagram of the following.
  - (*a*) L. S. Strobilus of ***Lycopodium***.
  - (*b*) T. S. Stem of ***Lycopodium***. **(Allahabad, 2000)**
  - (*c*) Prothallus (gametophyte) of ***Lycopodium clavatum***. **(Kanpur, 2001; Lucknow, 2000)**
  - (*d*) V. S. Gametophyte of ***Lycopodium cernuum***.
  - (*e*) T. S. ***Lycopodium clavatum*** stem.
  - (*f*) Strobilus of ***Lycopodium***.
  - (*g*) V. L. S. gametophyte of ***Lycopodium cernuum***.
  - (*h*) T. S. Root of ***Lycopodium***.
  - (*i*) T. S. Rhizome of ***Lycopodium***
  - (*j*) Sporophyte of ***Phylloglossum***.
  - (*k*) Gametophyte of ***Phylloglossum***.
  - (*l*) ***Lycopodium*** stem showing plectostele **(Kanpur, 2004)**

30. Answer the following going two important points:
  - (*a*) Antheridium of ***Lycopodium***.
  - (*b*) ***Lycopodium*** leaves.
  - (*c*) Structure of stele in ***Lycopodium*** roots.
  - (*d*) Sporangium of ***Lycopodium***.

31. (*a*) Trace the steler variations in ***Lycopodium***.
  - (*b*) Describe any type of gametophyte of ***Lycopodium***.

32. Compare the gametophyte of ***Lycopodium*** with that of ***Equisetum***.

33. What is the chromosome number of ***Lycopodium***?

34. Why are those species of ***Lycopodium*** which show the selago condition regarded as more primitive than the others?

35. Describe briefly the gametophyte of ***Phylloglossum***.

36. How does prothallus of ***Lycopodium*** reproduce vegetatively?

37. What is protocorm? Discuss its morphology. **(Kanpur, 2004)**

38. Explain the sporophyll of ***Lycopodium***. **(M.S. Univ., Tirun, 2005)**

39. Discuss the development of sex organs in ***Lycopodium***.

40. Explain the sporophyll of ***Lycopodium***. **(M.S. Univ., Tirun, 2005)**

41. Discuss the development of sex organs in ***Lycopodium***. **(M.S. Univ., Tirun., 2005)**

OBJECTIVE TYPE

42. Select the correct answer.

(*i*) In ***Lycopodium*** stem the stele is
  - (*a*) Solenostele
  - (*b*) Dictyostele
  - (*c*) Siphonostele
  - (*d*) Plectostele.

(*ii*) Protocorm formation occurs in
  - (*a*) ***Lycopodium***
  - (*b*) ***Selaginella***
  - (*c*) ***Equisetum***
  - (*d*) ***Marselia***.

(*iii*) Actinostele is found in
  - (*a*) ***Lycopodium cernuum***
  - (*b*) ***L. clavatum***
  - (*c*) ***L. serratum***
  - (*d*) ***L. phlegmaria***.

(*iv*) Plectostele is a type of stele present in
  - (*a*) ***Lycopodium***
  - (*b*) ***Selaginella***
  - (*c*) ***Equisetum***
  - (*d*) Marsilea.

(*v*) Mycorrhiza is found in the prothallus of
  - (*a*) ***Selaginella***
  - (*b*) ***Equisetum***
  - (*c*) ***Pteris***
  - (*d*) ***Lycopodium***.

(*vi*) ***Lycopodium*** produces the spermatozoids with
  - (*a*) Two flagella
  - (*b*) Four flagella
  - (*c*) Many flagella
  - (*d*) No flagella.

(*vii*) Biflagellate spermatozoids are found in
  - (*a*) ***Lycopodium***
  - (*b*) ***Selaginella***
  - (*c*) ***Equisetum***
  - (*d*) Pteris.

(*viii*) Stele in ***Lycopodium*** is
  - (*a*) Dictyostelic
  - (*d*) Protostelic
  - (*c*) Solenostelic
  - (*d*) Siphostelic.

(*ix*) On which side is the sporangium seen on the sporophyll in ***Lycopodium***?

(*a*) Abaxial

(*b*) Basal,

(*c*) Axillary

(*d*) Adaxial.

(*x*) Wall of sporangium in ***Lycopodium*** usually consists of

(*a*) Single layer

(*b*) Two layers

(*c*) Three layers

(*d*) Many layers.

(*xi*) ***Lycopodium*** is commonly called as

(*a*) Horsetail

(*b*) Club moss

(*c*) Quillwort

(*d*) Stonewort.

(*xii*) Fleshy tuber and underground portion of the sporophyte is characteristic of

(*a*) ***Lycopodium***

(*b*) ***Selaginella***

(*c*) ***Phylloglossum***

(*d*) ***Equiseatum.***

(*xiii*) Where is ***Phylloglossum*** found naturally?

(*a*) India

(*b*) England

(*c*) Russia

(*d*) Tasmania.

(*xiv*) In ***Phylloglossum*** the sporophylls are arranged on the axis

(*a*) Alternately

(*b*) Opposite to each other

(*c*) Without any definite pattern

(*d*) Sometimes alternately and sometimes opposite.

(*xv*) Spores are Tetrahedral in

(*a*) ***Lycopodium***

(*b*) ***Phylloglossum***

(*c*) ***Selaginella***

(*d*) ***Equisetum.***

(*xvi*) Homosporous condition is found in

(*a*) ***Lycopodium***

(*b*) ***Marsilea***

(*c*) ***Selaginella***

(*d*) ***Cycas***

(*xvii*) How many types of prothalli are found in different types of ***Lycopodium***?

(*a*) 1 (*b*) 2

(*c*) 3 (*d*) 4

(*xviii*) Many types of steles occur in

(*a*) ***Marsilea***

(*b*) ***Lycopodium***

(*c*) ***Rhynia***

(*d*) ***Equisetum***

Isoetes hystrix

CHAPTER 5

Lycophyta–Ligulopsida

- Isoetales–General
- Isoetales
- Description of ***Isoetes*** Linn
- Description of ***Stylites***
- Differences between ***Isoetes*** and ***Stylites.***

ISOETALES–General

It includes a single family **Isoetaceae**. ***Isoetes*** and ***Stylites*** are the living, and ***Isoetites*** is the extinct member of the family. The fossil history of the genus is meagre and on that account the living member ***Isoetes*** is regarded as an isolated type possibly of considerable antiquity and as pointed out by Seward and others closely akin to such extinct genera as ***Pleuromia*** and ***Sigillaria. Some*** species of the extinct genus ***Isoetites*** have been described but their identity is doubtful. Only ***Isoetites choffali*** described by Saporta from Lower Cretaceous of Portugal is slightly better known. ***Stylites*** has two species found in Peruvian Andes. It differs from ***Isoetes*** in having elongated stem and unbranched roots. Rauh and Falk reported it in 1959. ***Stylites andicola*** and ***S. gemmifera*** are the two species reported from central Peru.

ISOETES Linn.

It includes about 75 species (Airy Shaw in Willis 1966) that are familiarly known as **'quillworts'** due to their narrow and elongated grass-like leaves with broad and spathulate bases. Majority of the species are found in Europe and North America. In India, seven species have been recorded. The most common out of them is ***Isoetes coromandelina*** (Fig. 5.1). The others are ***I. samapathkumarani***, ***I. indica, I. mirzapurense***, ***I. panchananii***, ***I. dixetii*** and ***I. sahyadrii.*** Bierhost (1971) mentions 40 species.

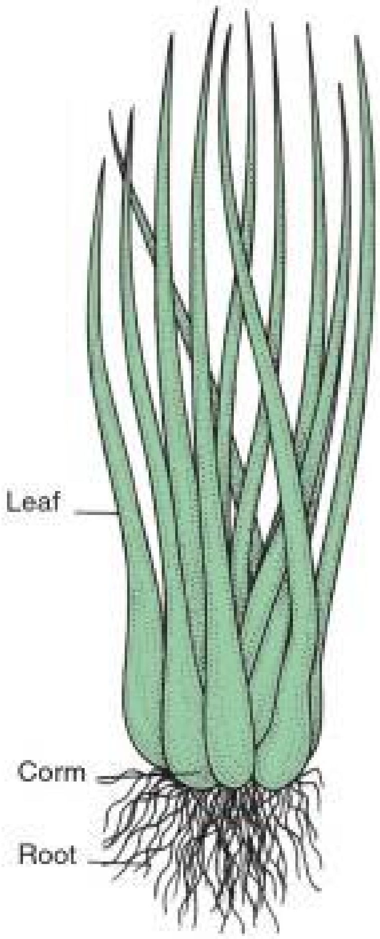


Fig. 5.1. *Isoetes coromandelina.* A complete plant showing habit.

The Sporophyte

Habit and Habitat

The common Indian species ***I. coromandelina*** grows wild along the Coromandel Coast, Madras, Kerala, Bombay, Varanasi, Baroda, Serampur in Bengal, along the banks of river Jamuna at Delhi, Allahabad, Rewa. Padampur, Eastern India, Lucknow, Faizabad, Indore and in an uncultivated land at Meerut. ***I. panchananii*** is very common at Pachmarhi (Bhambie and Sharma, 1956; Bir and Vasudeva, 1972, 1973). Pant and Srivastva (1962) have given a complete range of distribution of various species in India along with their distinguishing characters and key for identification. The Indian species are terrestrial as well as amphibious. ***Isoetes coromandelina*** is perennial with a distinct growing season that starts about mid-October after the monsoon and continues till March. It is mostly amphibious in existence and is common along the edges of ponds, pools and rivers. It also grows in shallow water with portion of leaves projecting above water. ***I. panchananii*** is also amphibious. The plants vary in size from 20 to 60 cms.

The America species ***I. englemanni*** is a partially submerged, aquatic ***Isoetes japonica*** grows submerged in water. ***I. butleri*** is terrestrial.

The sporophyte of ***Isoetes***, when growing under natural conditions, gives the appearance of a liliaceous or a graminaceous monocotyledon due to its characteristic linear leaves that arise from a subterranean and bulbous axis (Fig. 5.1). The underground portion of sporophyte has been given the names of "Corm" and 'rhizome', because it is thick, reduced and looks like a condensed rhizome. Eames

Isoetes coromandelina

(1936) uses the term **axis** for this underground stem like part. The axis is clearly distinguishable into an upper leaf bearing part and a lower portion which bears the lateral roots. The former is called the **stem** and latter as **rhizomorph**. Since the axis is greatly reduced the leaves and roots appear to arise very close to each other and the line of demarcation between the **stem** and the **rhizomorph** is obscure.

I. butleri

Axis

In young plants the axis is more or less globular and is covered with the leaves at its top and roots at its lower parts (Figs. 5.1 and 5.2). In older plants it becomes lobed. The number of lobes vary from two or three and even four or five in rare cases (***I. saccharata*).** The grooves between the lobes deepen as the axis increases in age and make them (lobes) prominent (Fig. 5.2). Brongniart (1828) related the lobed axis of ***Isoetes*** to the ***Stigmarian*** axis. This view is not valid as the lobes in ***Isoetes*** do not develop due to the action of supplementary vegetative cones at the basal side (as in ***Stigmaria***), but only due to the local formation of the secondary tissues by the cambium. Bhambie (1965) reported plants of ***I. coromandelina*** with four lobed axis. According to him this condition is quite prevalent in this species and appears to be a normal feature. The shape of the axis in such plants is roughly cylindrical in the upper and measures about 1.5 cm. in diameter. Such four lobed axes of ***Isoetes*** has been compared with those of fossil lycopods like ***Pleuromia*** and the stigmarian base. In the words of Bhambie (1965), "though the stelar lobes in ***Isoetes*** do not coincide with those of the cortical lobes of the axis, the four lobed axes of ***I. coromandelina*** show more resemblance with the basal region of ***Pleuromia*** and stigmarian base". Four or even Five lobed axes have also been reported in some other species ***e.g. I. lacustris***.

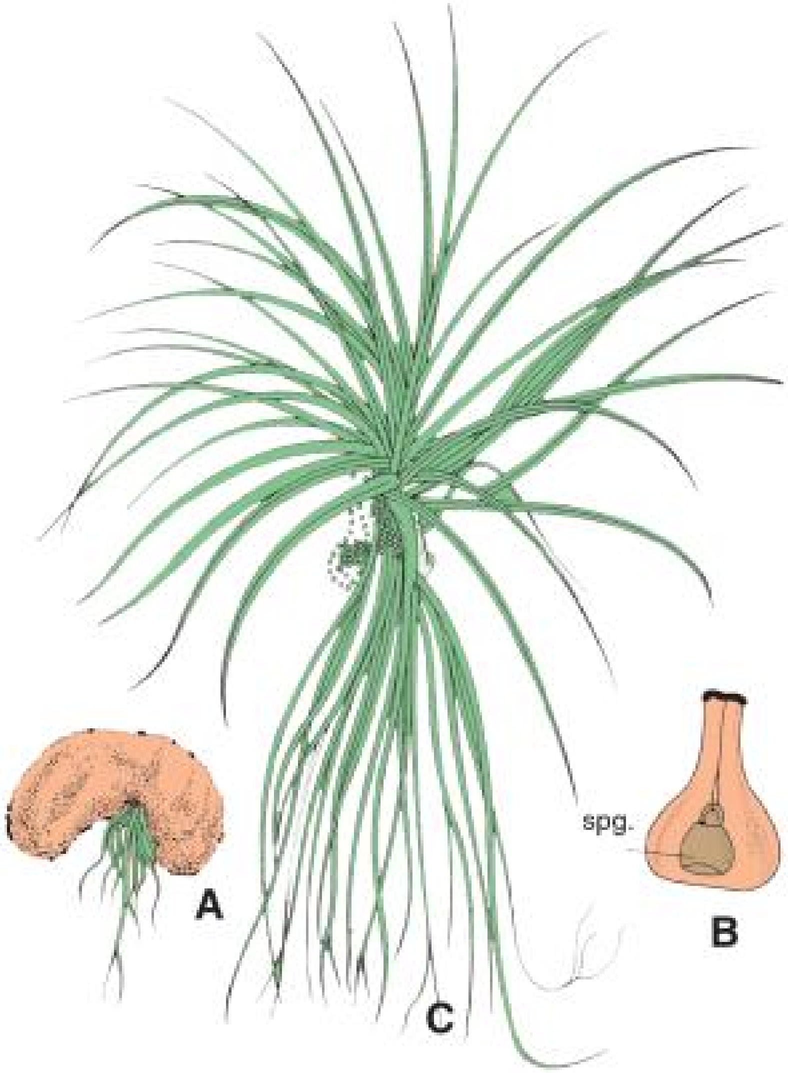


Fig. 5.1a (A—C). **A.** Axis of ***I. lacustris.*** Note the lobes and dichotomously branched roots; **B. Base of sporophyll of I. *lacustris.*** l, ligule ; spg., sporangium partially covered by velum; **C.** A complete plant of ***I. echinospora*** (After Motelay and Vendryes)

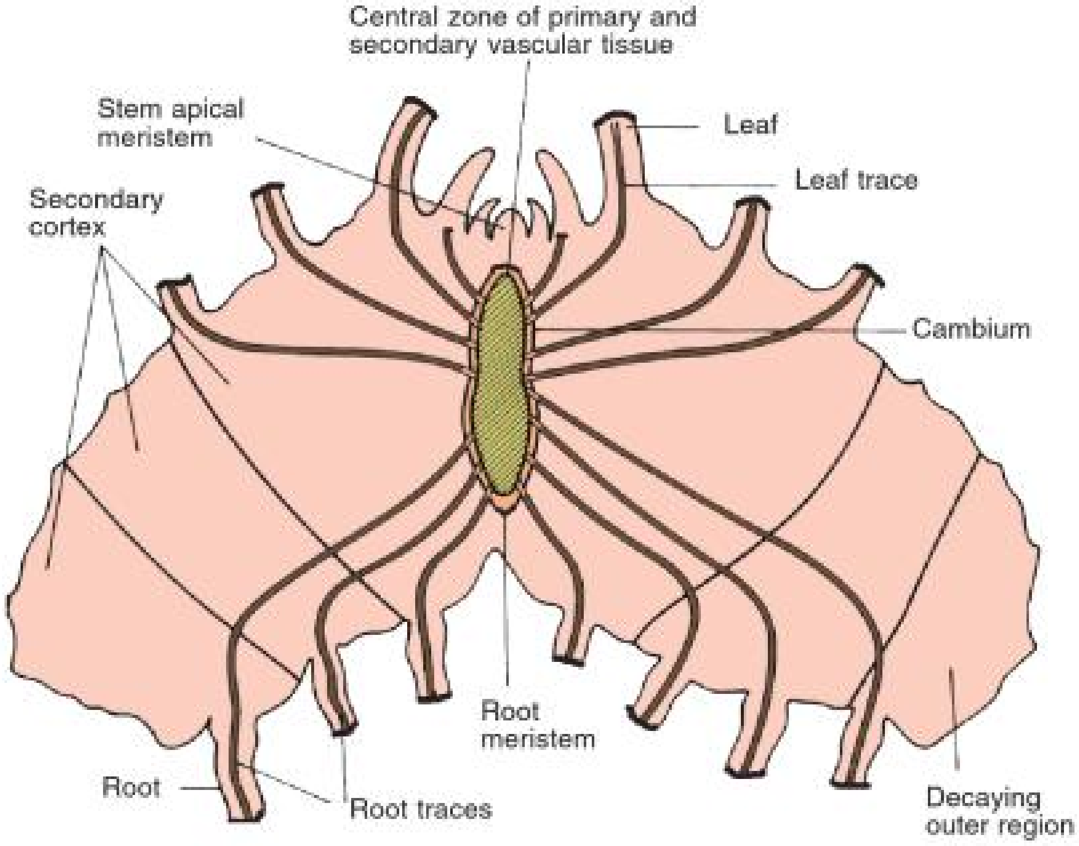


Fig. 5.2. ***Isoetes coromandelina.*** V. S. through the axis (diagrammatic) showing internal organisation.

The place where the lobes arise is determined by the phyllotaxis of the young plants. In distichous plants the grooves alternate with the leaf orthostichies under which the lobes are formed. Such a position was first observed by A.L. Braun in 1847. Once the lobes are formed they maintain their position even on change of phyllotaxis. The lobes grow more in breadth by the dilatation of the tissue and vary from 0.5—4 centimetres in width. Grooves develop by the appearance of longitudinal slits between the lobes. The tissues are sloughed off in the form of characteristic 'caps or shoulders' (Eames, 1936) that appear on the upper margins of the axis (Fig. 5.2). This sloughed off tissue includes the bases of the leaves and the roots of the previous year and undergoes decay at the end of the growing season. The growth in length of the axis is very slow and is effected by a group of the meristematic cells that lie sunken in a groove formed by the greater growth of the surrounding tissue.

Karrfalt and Eggert (1972) studied the development of roots and lobes in some species of ***Isoetes*** (***I. saccharata*** and ***I. tickermanni***). They ascribe their formation to two developmental processes. They found that there is a row of tangentially elongated cells at the base of the furrows. They perform the mechanical function of separating the lobes. " Progressive rupture of these cells from surface to deeper layers maintains the depth of the furrow. This layer of elongated cells becomes double and by meristematic activity produces a new lobe in the region between the two layers. New lobes also appear by the development of a furrow between the two bands."

Dichotomous branching has also been observed in some plants, but the dichotomy never becomes prominent due to the very slow growth of the axis. It is evident only by the presence of two crowns of leaves.

Morphological Nature of the Axis

Regarding the morphological nature of the axis, several views have been advanced. Braun (1847) believed that the lower part of the ***Isoetes*** stock base was nothing but a telescoped main root.

He based his view on the basipetalous development of the new roots. Scott and Hill (1900) studied the development of roots in ***I. hystrix*** and disagreed with Braun. Lang (1915) after intensive anatomical studies concluded "that the recognition of the lower region of the stock of ***Isoetes*** as a rhizomorph in some way correlated with the upwardly growing shoot appears to be justified". Liebig (1931) declared that all her median longitudinal sections of the stock are proofs of Braun's thesis. West and Takeda (1915) hold another view. They regard the downward growing rhizomorph as an organ ***suigeneris***. Eames (1936) regards the axis as differentiated into an upper leaf bearing portion called the **stem** and a lower root bearing portion called the **rhizomorph**. Schoute (1938) regards the ***Isoetes*** axis as a stem and states "....that the stock base of ***Isoetes*** is peculiar in its constantly tearing furrows, a feature connected with the formation of local humps of secondary tissue, the lobes. Roots are formed ,as always in all plants, in any suitable place; the presence of the furrows and the lack of new higher stem parts cause these suitable places to be found in an unusual arrangement." He used the term stock base for the axis.

Bhambie (1970) has considered the morphology of the **rhizomorph** in detail and has given a vivid picture of the various views presented by different authors. He has considered this problem under five headings as : (***a***) it is a secondary product of cambium activity, (***b***) it is partly or wholly formed by the fusion of the basal portion of roots, (***c***) it is a root, (***d***) it is an organ ***sui generis*** and (***e***) it is shoot like in nature.

(a) Secondary product of Cambial Activity

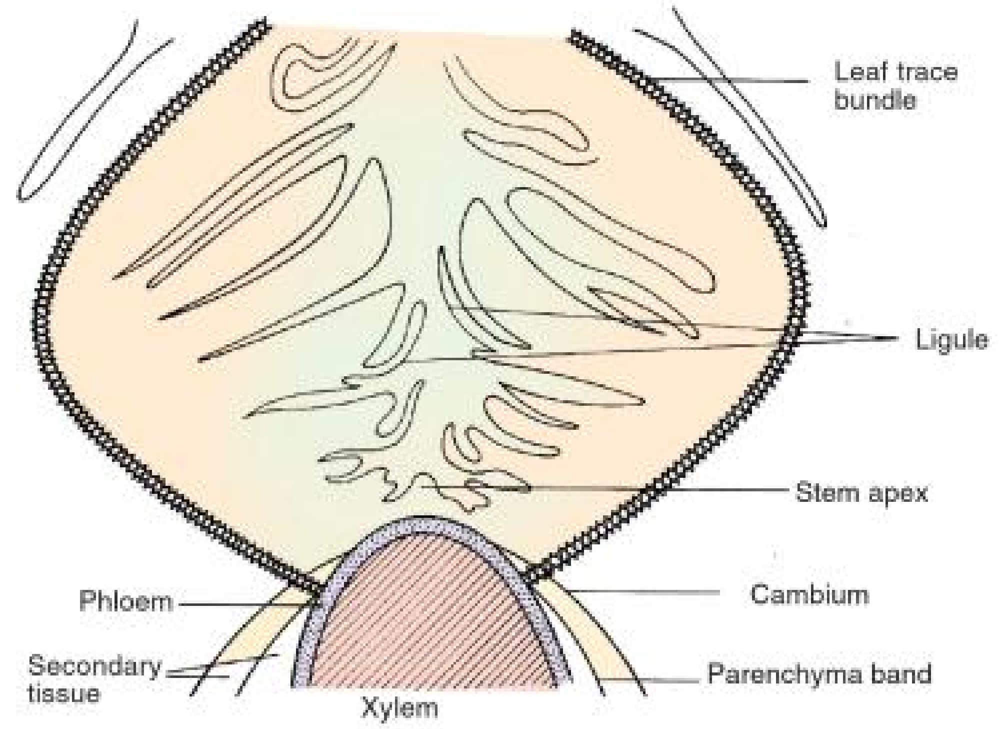


Fig. 5.3. ***Isoetes coromandelina.*** L. S. Through the axis (upper part) showing the stem apex, vascular region and arrangement of young leaves. Also note the ligules. (After Bhambie)

The proponents of this view believe that rhizomorph is a product of secondary activity and is formed by the cambial activity of the plant. Hofmeister (1862) and Schoute (1938) support this hypothesis. Hofmeister did not consider rhizomorph as a fundamental part of the plant body and regarded it as later development due to cambial activity. Schoute also regarded the rhizomorph lobes as humps of tissue formed by cambial activity. Anatomical studies (Bhambie, 1957, 1962, 1970) have revealed that the stele of the axis is anchor-shaped and has two distinct regions : (***i***) The upper region which is cylindrical and forms the stem stele and gives off leaf traces and (***ii***) the rhizomorphic stele which sends off roots traces and is bi-,tri, or tetra- radiate depending upon the number of lobes of the rhizomorph. Both the steles are connected in the central region of the axis. The lobes of the rhizomorphic stele have upturned free ends that alternate with the cortical ridges of the axis and centrally fused. Three distinct types of meristems have been recognised. These are : (***i***) the apical meristem which forms the stems stele;

(***ii***) the lateral meristem which originates in periphery of the primary phloem and completely surrounds the stem stele and is located in the form of strips between the rhizomorphic lobes and (***iii***) the basal meristem present all along the ridges of the rhizomorphic stele. It adds new tissue to the rhizomorphic stele (Bhambie 1962) and gives rise to the roots also. It extends upto the upturned edges of the rhizomorhpic stele. The stem and the rhizomorph have their own meristem. In the light of these observations it is difficult to believe that the rhizomorph is a new structure and is not a fundamental part of the plant body.

(*b*) *Fusion product of Roots*

This view was put forward by Sachs (1882) and De Bary (1884) and later modified by Scott and Hill (1900). Sachs and De Bary were of the opinion that the rhizomorph is formed by the fusion of the basal parts of the roots whereas Scott and Hill believed that it is partly formed by the fusion of the bases of roots and partly by the activity of the cambium. The view has been opposed by Bhambie who is of the opinion that the anatomical studies strongly support that rhizomorph is a "solid structure having its own entity." He further remarks, " Moreover, the root primordia arise just below the rhizomorph and later their steles become connected with the stele of the rhizomorph (Bhambie, 1963 b)."

(*c*) *Organ Sui-genesis*

This view was put forward first by West and Takeda (1915) and later supported by Bowers (1935), Sporn (1963) and Wardlaw (1965). They believed that rhizomorph is neither a stem nor a root, but an organ of indeterminate character.

(*d*) *Root like nature*

It was proposed by Stokey (1909) who stated that the tuberous body (axis) is not wholly stem but a "contracted stem and main root". She has not given any anatomical reasons for such a conclusion. The present day studies on the anatomy of the rhizomorph do not support such a conclusion.

(*e*) *Shoot like nature*

This view was first put forward by Von Mohl (1840) who regarded the rhizomorph as a descending organ of the axis which gives rise to the roots. Lang (1915) regarded it as a downwardly growing rhizophore whose apex behaves like the stem apex. Eames (1936) also regarded it as resembling the rhizophore which is shoot like in nature. Seward (1910), Smith (1955), Stewart (1947) and Andrews (1961) also regard it as shoot like in nature. Laclercq (1930), Weiss (1931-32), Eames (1936), Andrews (1961) and Philips and Gilbert (1966) compared the rhizomorph of **Isoetes** with root bearing regions of some fossil lycopods and confirmed the shoot like nature of this structure. Bhambie (1970) also agrees with the proponents of axial nature of the rhizomorph. His conclusions are based on the detailed anatomical studies of the genus.

GROWTH

There are two schools of thought regarding the organisation of the shoot apex in ***Isoetes***. These are :

Apical Cell Hypothesis

It was put forward by De Bary (1884), Hofmeister (1862) and Nageli (1878). These botanists asserted that there is a single apical cell at the apex of the axis. This was later supported by Van Tiegham (1891), Scot and Hill (1900) and by Karrfalt (1977) in the shoot apex of ***I. hystrix.***

Many-celled Meristem Hypothesis

Hegelmaier (1874) described the presence of a superficial meristematic layer. Farmer (1890) observed a single layer of columnar cells covering the entire stem apex in ***I. lacustris***. Smith (1900), West and Takeda (1915) and Lang (1915 a, 1916 b) also observed a group of meristematic cells at the shoot apex. Paolillo (1963) and Bierhorst (1971) described that there is a dome of meristematic cells having a few centrally located apical initials at the crest as in ***Lycopodium*** that are responsible for the growth of the plant. Bhambie (1957, 1972, 1988) studied the shoot apex in ***I. coromandelina*** and ***I. englemanni*** and discovered a hump of meristematic cells. He distinguished two more or less well demarcated regions in this apical hump. A superficial layer of columnar meristematic cells that divide mainly by anticlinal divisions and an inner tissue that divides in an irregular fashion. Histochemical studies in ***I. setcea*** by Michaux Ferriere (1976 - 1978) have confirmed Bhambie's observations.

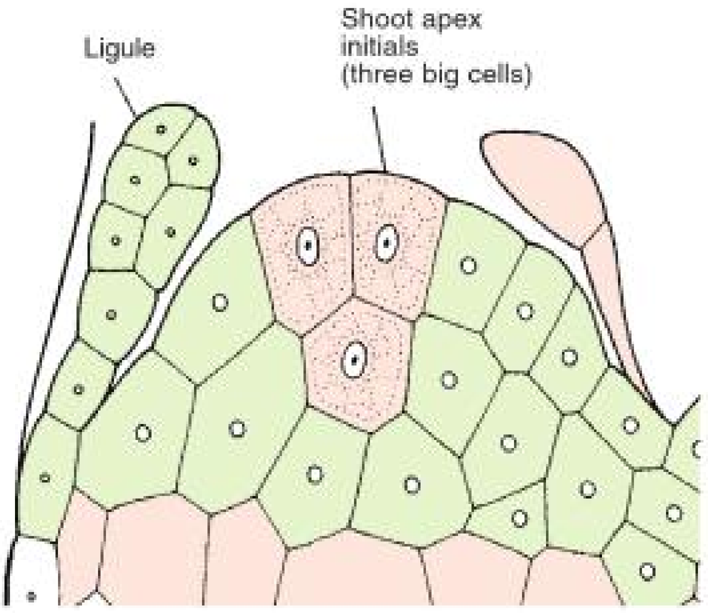


Fig. 5.4. *Isoetes sampathkumarani.* A section through stem apex showing three big shoot apex initials. (After Usha Sharma)

Usha Sharma (1960) studied the shoot apex in ***Isoetes sampathkumarani*** and observed a superficial layer of meristematic cells that divide anticlinally and give rise to the outer epidermal layer (Fig. 5.4). She also observed an inner mass of irregularly dividing cells. For a detailed information on the apical meristems in pteridophytes reference may be made to Bhambie, S. and V. Puri (1985, Trends Pl. Res. pp. 55-81).

Root

In the embryo the first root arises laterally and exogenously (Farmer, 1890). It is provided with root hair and with a root cap. The position of the later roots that arise endogenously is always related to the place of the grooves. These roots, according to most of the authors, are formed in series along the sides of the grooves and are, therefore, in the same position as the orthostichies. This is because the grooves appear in the same position as the orthostichies. In each groove or a furrow the roots arise in an acropetalous succession, ***i.e.***, the youngest is near the stem apex or the end of the groove. West and Takeda (1915) reported that all the roots in furrow are of the same age—a statement that is very difficult to believe. They have not given any observations in support of their statement. Scott and Hill (1900) have clearly shown the acropetalous development of the roots in ***I. hystix.*** West and Takeda state that in ***I. japonica*** new roots develop on the sides of the grooves near the base . When new roots develop in the next season the older ones are pushed outwards towards the ends of the groove (stem apex). Accordingly the younger roots are near the centre of the groove and older ones at the ends of the grooves.

I. hystix.

I. japonica

The roots branch dichotomously after emerging from the **rhizomorph** (lower part of the axis) ground tissue. The root apex has been reported to consist of a group of initials (Farmer, 1890, Campbell, 1891) that give rise to the root cap, epidermis and cortex. According to these authors, the vascular tissues arise from a single initial. According to Bhambie (1963, 1985 p. 68) the root apex "has a group of centrally located inconspicuous initials which produce a cap distally and a body of the root proximally. The root cap has a columella." For details refer to Bhambie and Puri (1985).

Leaf

The leaves are microphyllous as they are traversed by a single median and unbranched vein. The leaf traces leave no gap in the vascular cylinder of the stem. They vary in length from two centimetres to two feet (***I. englemanni***). They are arranged in close spirals near the upper end of the axis, and range in number from a few to 20. Each leaf has a broad spoon-like base and a narrow and linear upper part. The leaf tips are pointed and straight or recurved and sometimes four-angled. The basal, broad portions of the leaves are underground and colourless, whereas the aerial and linear parts are green and photosynthetic. The leaf bases of outer leaves overlap those of the inner leaves and thus give a bulbous appearance (Fig. 5.1). Usually the first formed or the older leaves and those produced at the end of the growing season are sterile and the rest are fertile, ***i.e.***, they bear sporangia and are called **sporophylls**. In some species abortive sporangia have also been noted at the bases of the sterile leaves. So every leaf is a potential sporophyll and the entire plant can be regarded as a **strobi-**

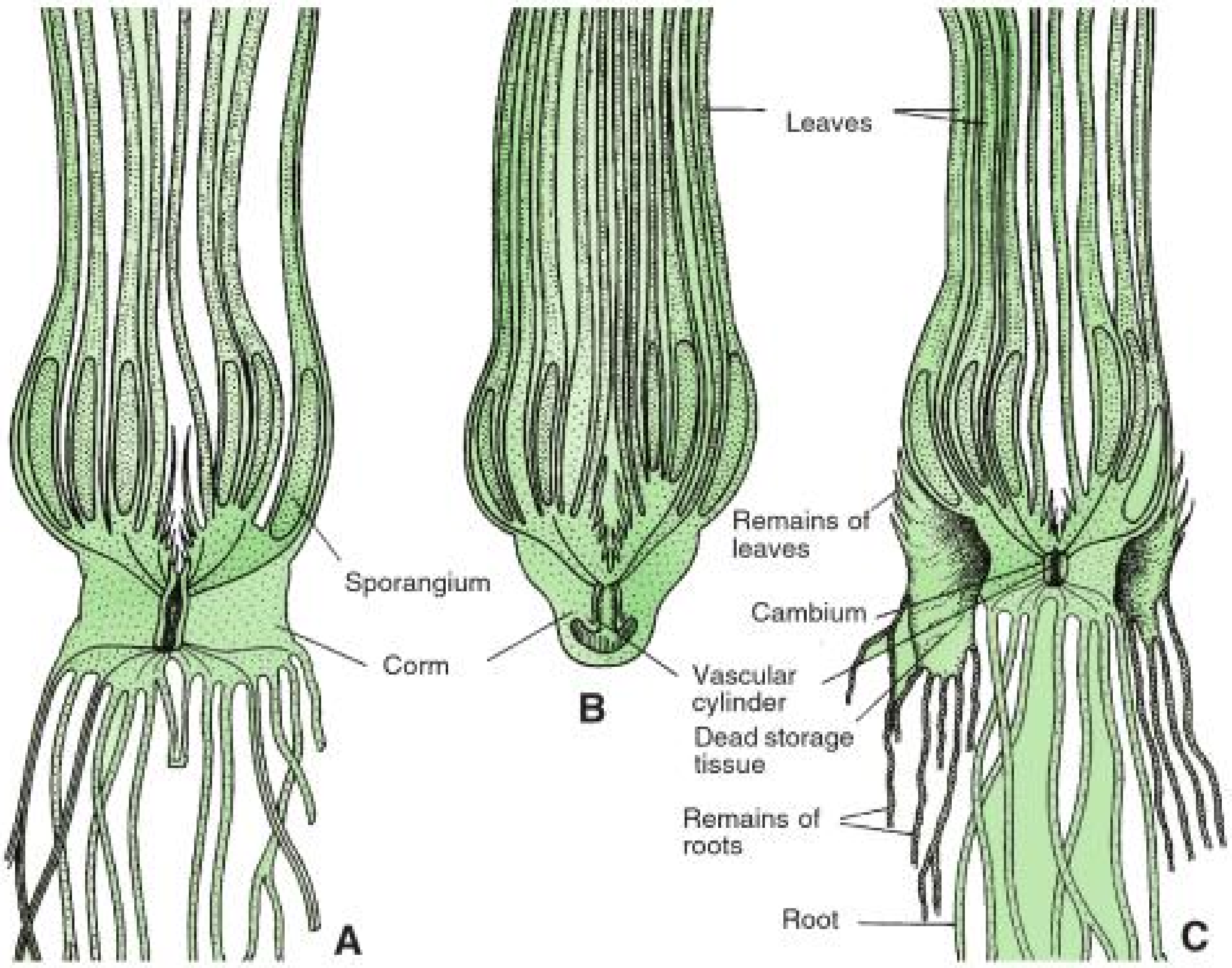


Fig. 5.5 (A-C). V. S. diagrams through the entire plant of ***I. coromandelina*** illustrating form and structure. **A.** V. S. cut at right angles to the basal groove of the "corm" of a young plant, showing sporangia, the apex and the stele of the corm; **B.** V. S. of the plant showing part of the groove where the stele appears like an inverted 'T'; **C.** Same as A but the plant is older and shows storage region of the corm and dead remains of older tissue.

lus. Each leaf has, therefore, a lower colourless sporangium bearing region (Fig. 5.5) or fertile region and an upper sterile or photosynthetic region. At the junction of the basal, spoon-shaped part of the leaf and the upper green part or the blade there is a small depression on the adaxial side. From this pit or depression arises a small ligule (Fig. 5.6).

Development of Leaf and Ligule

Leaves originate as small outgrowths that arise by the periclinal divisions of the surface cells of the apical meristem. The outgrowth assumes a crescentic outline in the beginning and soon a group of apical initials appears and initiates growth in length. During earlier stages of growth when the leaf mound is only few cells high, a prominent cell distinguishes itself on the adaxial side near the base of the leaf mound. This cell is the initial of the **ligule** (Smith, 1900). This cell divides periclinally and by repeated division gives rise to a filamentous structure that soon grows longer than the leaf primordium (Fig. 5.7, A). Later this filamentous structure, by divisions in various planes and by cell differentiation assumes a tongue-shaped form and shows highly specialised internal structure (Figs. 5.7 and 5.11). The base or the foot of the ligule is to some extent socketed in the tissue of the leaf. This socketed part is covered by a sheath that consists of a single layer of cells continuous externally with the leaf epidermis and internally with the epidermis of the ligule. Dunlop (1949) reported the presence of **casparian strips** in the cells of the sheath in ***I. macrospora.***

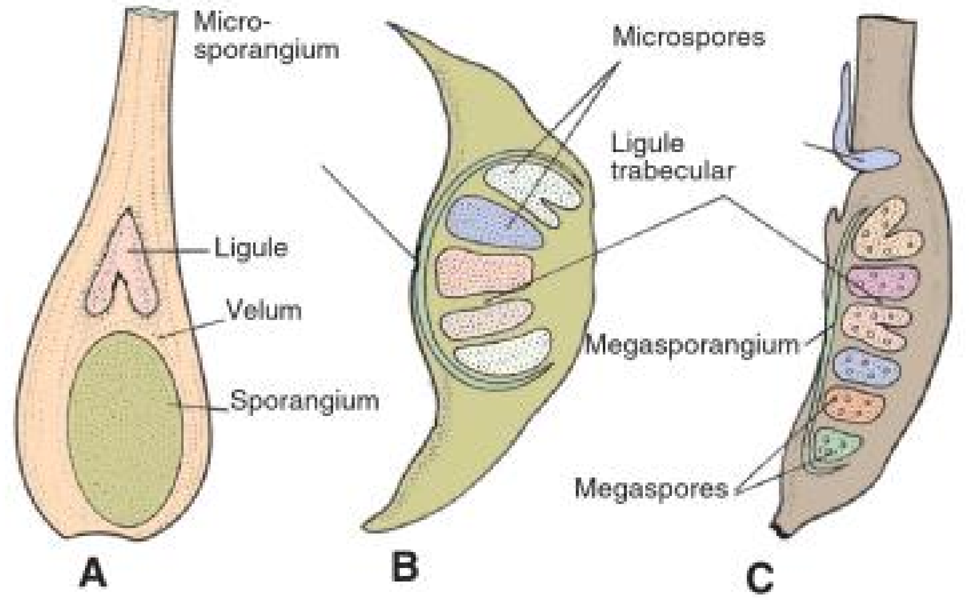


Fig. 5.6. *Isoetes.* **A.** Lower portion of the leaf showing ligule and the velum covering the sporangium; **B.** T. S. through the sporangial region of the microsporophyll showing a microsporangium with trabeculae; **C.** L. S. through the megasporangial part of a megasporophyall. Note the ligule and the velum.

The ligules are regarded as secretory structures that secrete water or mucilage and keep the leaves and the sporangia moist.

ANATOMY

Axis (Fig. 5.6a, A—D, Fig. 5.2,5.3, 5.5)

As stated before, the leaf bearing region of the axis is called **stem.** It has its own growing point called the **apical meristem**. The lower root bearing part which is called the **rhizomorph** also has its own growing point called the **basal meristem** or the **root meristem**. Growth in length of the axis is very slow, but increase in diameter is considerable. This circumferential increase is due to the activity of cambium also called the lateral meristem ***i.e.***, this axis exhibits secondary growth. The anatomy of the axis is complicated and is variously interpreted. The stelar arrangement in the axis is typically

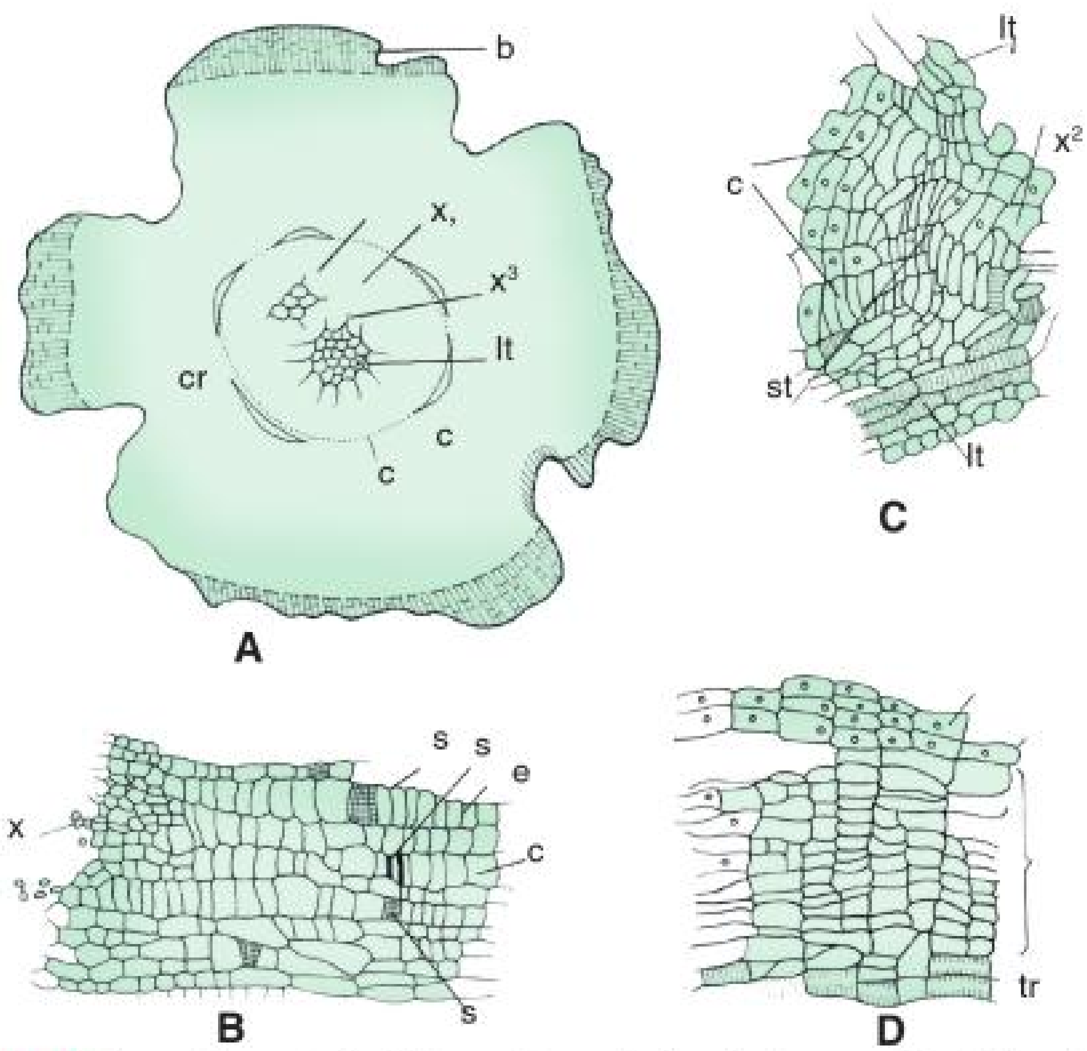


Fig. 5.6a (A—D) ***Isoetes lacustris.*** **A.** T.S. stem (upper leaf producing part of axis) showing epidermis (b), cortex (cr) extra stelar cambium (c), central stele (x), leaf traces (lt) xylem (x, x^2) and parenchyma zone (a) internal to cambium; **B.** L.S. portion of A showing cambium (c), phloem (s) and xylem (x); **C.** T.S. portion of A showing cambium (c), xylem (x, x^1), leaf traces (lt); **D.** T.S. portion of stem showing details of cambium and its derivative cells (d) and tracheids (tr). The derivative cells will distinguish into secondary phloem and xylem elements. (From Seward)

protostelic with a central core made up of xylem (tracheids and parenchyma) surrounded by phloem, which in turn is surrounded by an extra stelar layer of cambium. External to the cambium are the cortex and epidermis. The stele of the axis in a longitudinal section appears like an inverted 'T' or is anchor-shaped (Fig. 5.5 B). The vertical arm of the 'T' represents the stele of the upper region of the axis (stem) and the horizontal arm represents the stele of the rhizomorph. There is a prominent constriction between the two steles (Fig. 5.2 and 5.5 B). The xylem is composed of tracheids and xylem parenchyma. The phloem is made up of a few layers of prismatic cells. The cambium is absent opposite the apical meristems of stem and the rhizomorph and is, therefore, not a complete cylinder (Fig. 5.2)

The extra-stelar cambium which originates very early, cuts off cells both towards its inner side and outer side. (Fig. 5.2). Those cut off towards the inner side become changed into phloem (West & Takeda, 1915) or sometimes into phloem and xylem elements both (Scott and Hill, 1900). In some species the inner cells cut off by the cambium develop into tracheids and parenchyma (Stokey, 1909). Esau (1953) examined the cells cut off towards the inner side in ***I. howellii*** and found them to be secondary phloem. The **sieve cells have sieve areas** on their lateral and end walls.

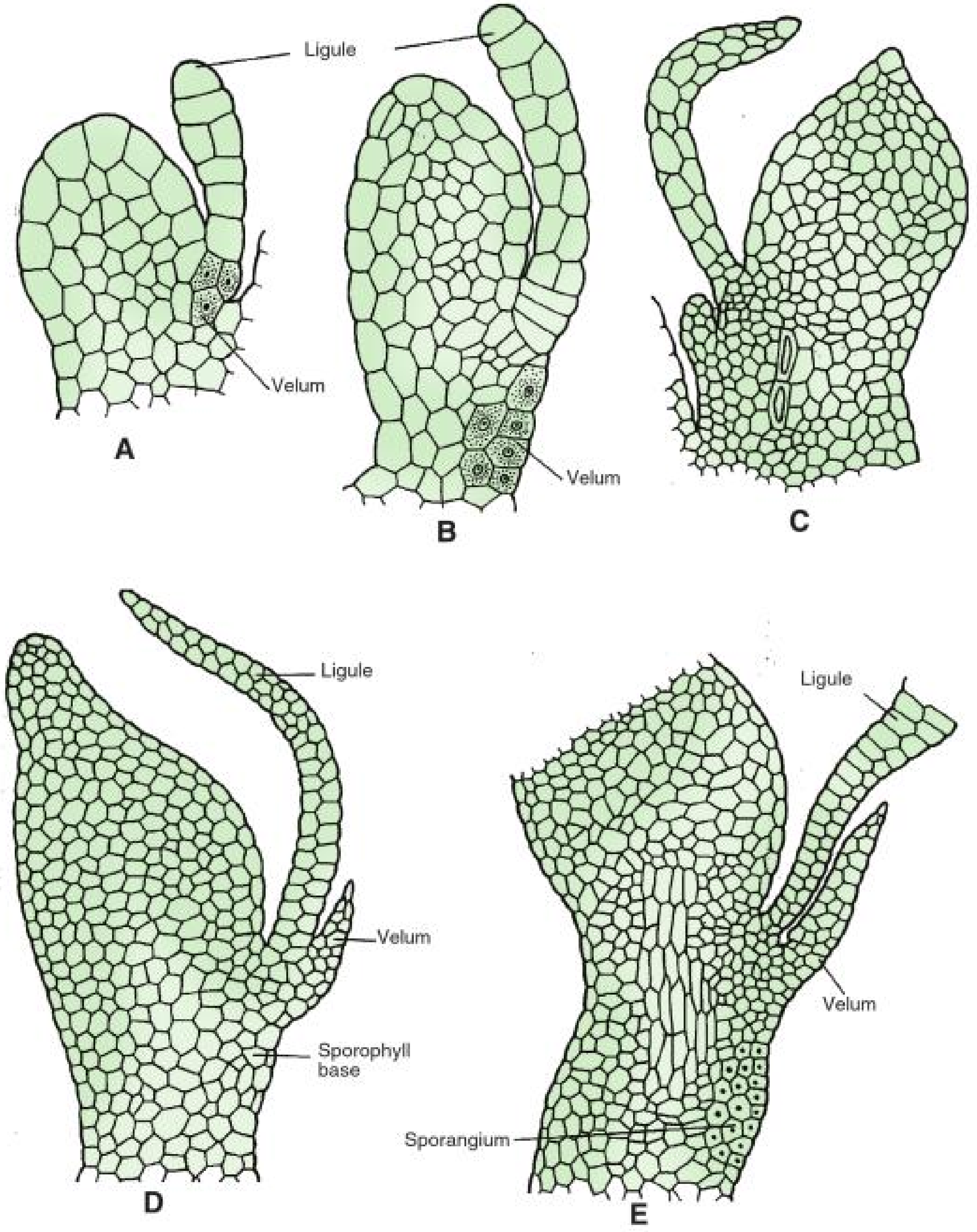

Ligule
Velum
A
Ligule
Velum
B
C
Ligule
Velum
Sporophyll base
D
Ligule
Velum
Sporangium
E

Fig. 5.7. (A—E). *Isoetes coromandelina.* Various stages in the development of the ligule and the velum. A younger sporangium is also seen developing below the velum in E. (After Ekambaram and Venkatanathan.)

The cells cut off towards the outer side develop into secondary cortex. The cells of the secondary cortex store food material and form the storage parenchyma. Every year new storage parenchyma is formed by the cambium and the older one is pushed outward and is ultimately sloughed off as characteristic 'caps' or 'shoulders'. The sloughed off tissue also includes portions of secondary vascular tissue. The surface layers that persist become suberised. Numerous leaf traces arise from the stele of the stem, one going to each leaf (Fig. 5.2). In the rhizomorph root traces pass from the stele to the roots (Fig. 5.2). The root traces are formed by the activity of the basal meristem or the root producing meristem. According to Bhambie (1962), this meristem also produces the elements of the stele of the rhizomorph.

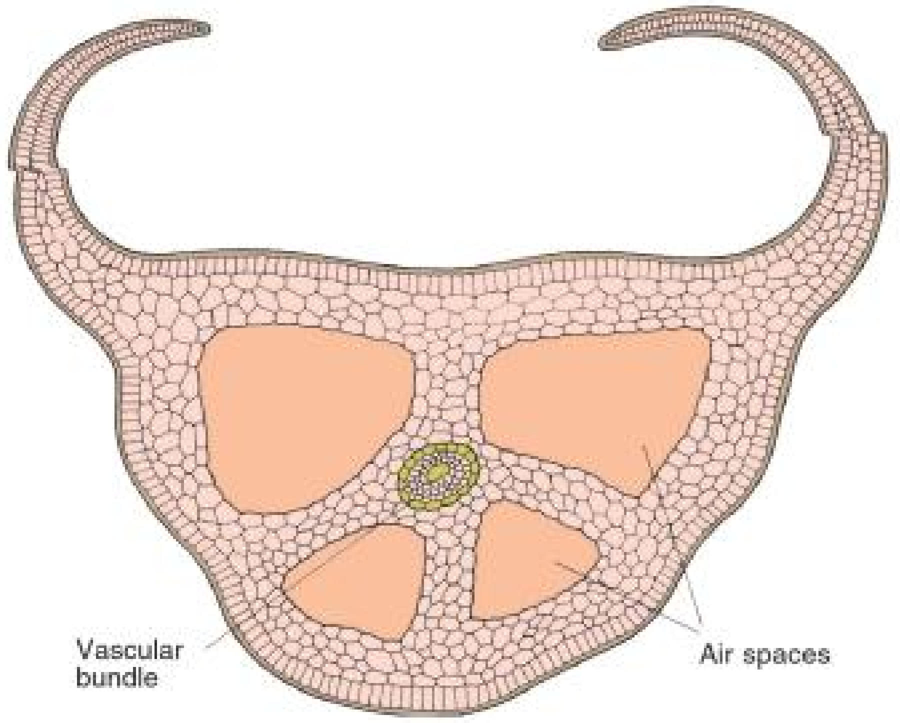


Fig. 5.8. *Isoetes coromandelina.* T.S. through leaf.

Leaf

A transverse section of the leaf (Fig. 5.8) shows an outer layer of compactly arranged cells called the **epidermis**. It is covered by a thin cuticle. Next to it is the mesophyll that is not differentiated into palisade and spongy parenchyma. The cells contain chloroplasts (Fig. 5.9) which range in number from one to four per cell. The chloroplasts are very close to the nucleus. The mesophyll is traversed by four longitudinal air spaces that are separated from each other by several layered thick partitions. The air spaces or the lacunae are divided by a series of partitions or diaphragms (Fig. 5.8). There is a single central collateral vascular bundle.

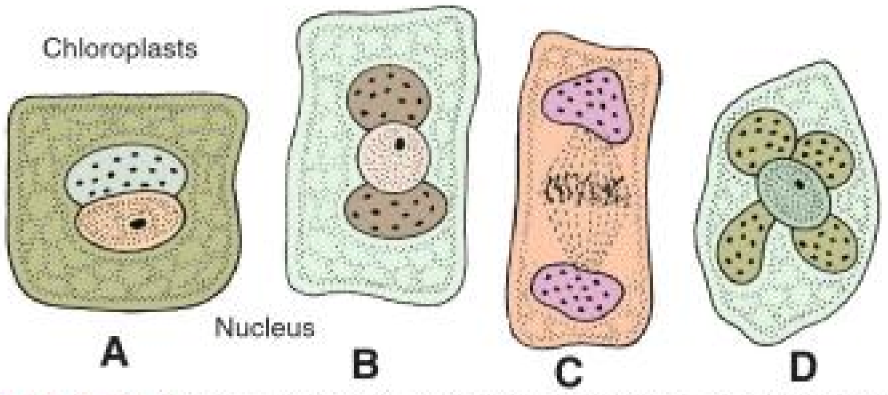


Fig. 5.9 (A-D). *Isoetes melanopoda.* **A.** Cell from a leaf with the chloroplast; **B.** Cell with two chloroplasts; **C.** same as B; **D.** Cell with four chloroplasts. (After Ma)

In the young sporophytes the leaf has only two lacunae. In the submerged species the epidermis lacks stomata whereas in the amphibious and terrestrial species stomata are present.

Root

A transverse section of a root (Fig. 5.10) reveals the usual tissue systems, ***viz.***, the epidermis, the cortex, the endodermis and the stele. The **epidermis** is single layered and temporary. The

cortex is made up of many layers of thin-walled cells and its innermost layer is called the **endodermis**. The endodermis possesses distinct **casparian strips**. The cortex surrounds a large air cavity. (Fig. 5.10).

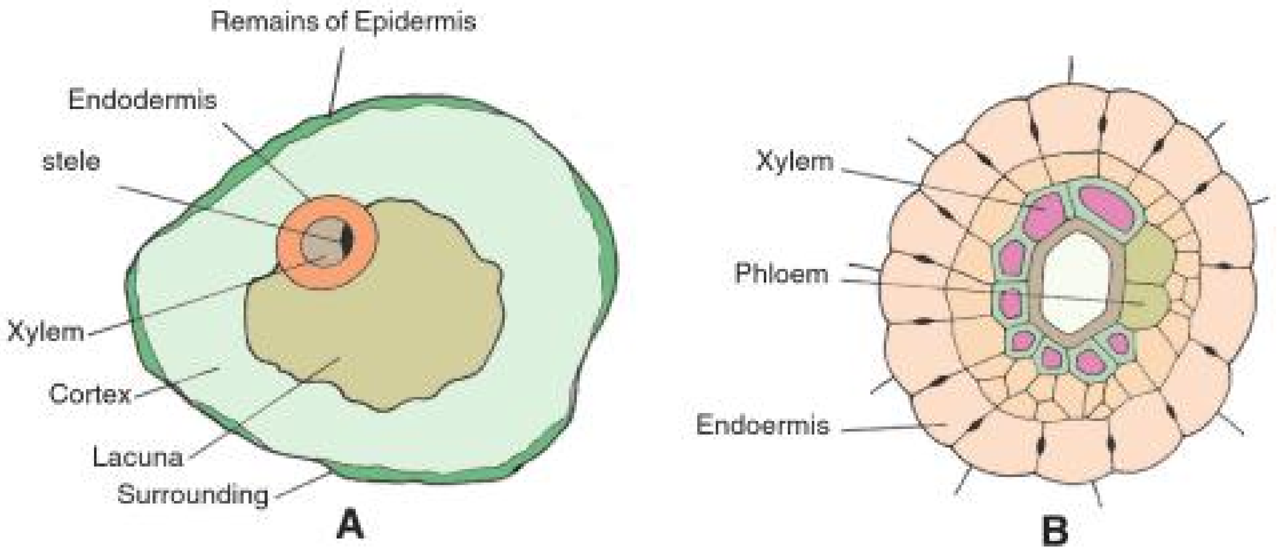
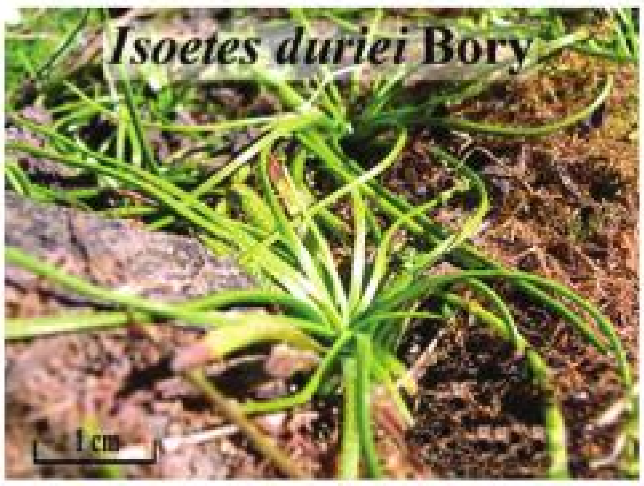


Fig. 5.10 (A-B). Root of *Isoetes sp.* A. A diagrammatic cross-section showing internal structure; **B.** stele shown in detail.

The vascular cylinder is present on one side of the cavity and is attached to the cortex on that side (Fig. 5.10). The stele consists of primary xylem and phloem that are collateral in arrangement. The phloem is oriented towards the cavity.



Isoetes duriei

Vegetative Propagation

Vegetative propagation is rare in ***Isoetes***. Formation of adventitious buds has been reported in some species. Solms-Laubach (1902) was able to induce the formation of adventitious buds in ***Isoetes lacustris*** and ***I. duriei.***

REPRODUCTION

The sporophyte is **heterosporous**. The **microsporangia** and **megasporangia** arise at the bases of **microsporophylls** and **megasporophylls** (Fig. 5.5). The megasporophylls form the outermost whorl (Fig. 5.5) and are followed by an inner whorl of microsporophylls which in turn surround the innermost sterile leaves that may in some species bear abortive sporangia. At the end of the growing season and during the resting period the megasporophylls and the microsporophylls degenerate or die whereas the innermost sterile leaves may continue to live. They act as outermost whorl during the next season and generally disappear before the new leaves appear.

Arrangement of Sporophylls

The arrangement of sporophylls has been studied in detail in some species by various authors. A brief resume is given here. The Indian species ***Isoetes coromandelina*** is very interesting. The first account of the arrangement of sporophylls in the species was given by Pfeiffer (1922). She found that majority of the plants bore only megasporophylls. In some specimens she found groups of microspores

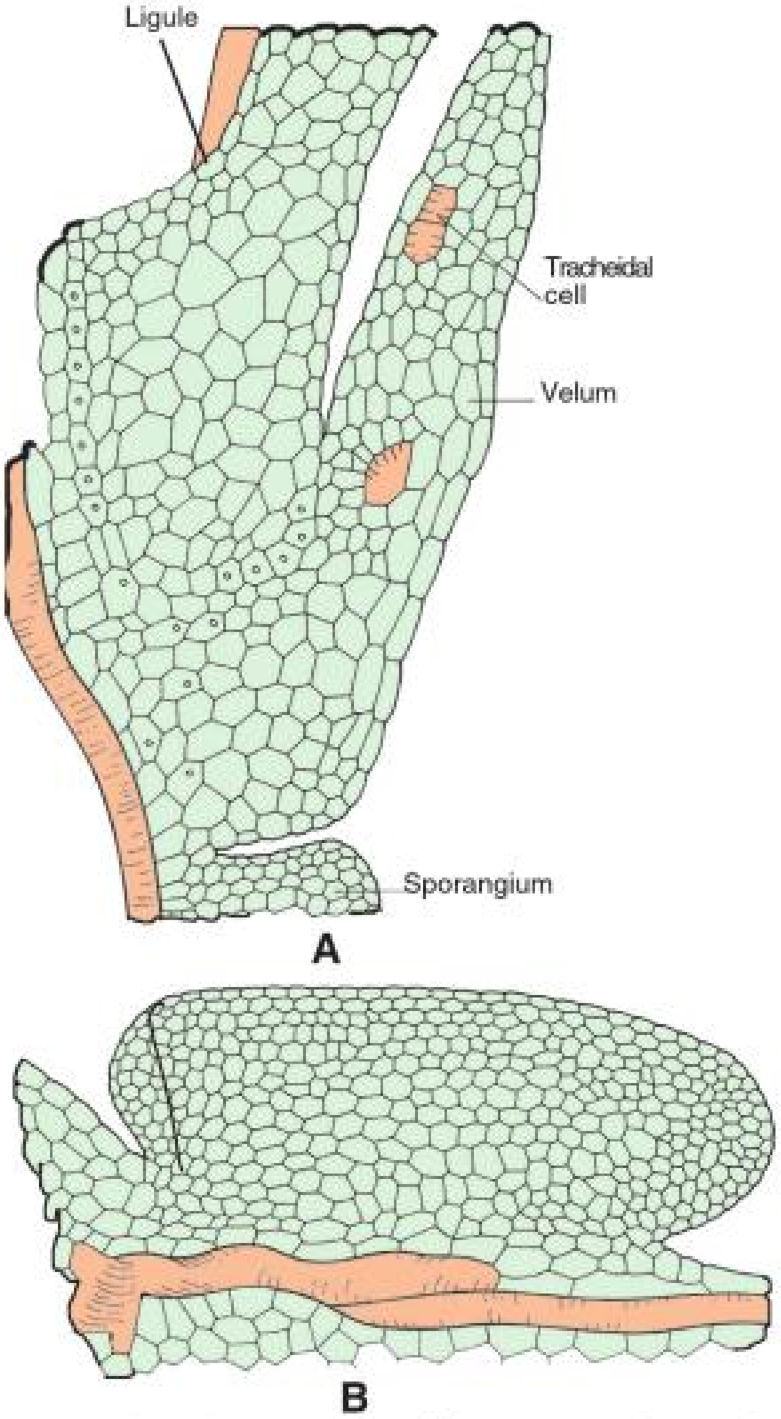


Fig. 5.11 (A—B). ***Isoetes coromandelina*.** **A.** portion of a sporophyll (in Longitudinal section) showing a portion of ligule, velum and upper part of sporangium; **B.** A young sporangium in section. There is no distinction of internal tissues. (After Ekambaram and Venkatanathan)

sticking to the bases of sporophylls. She was unable to observe the complete and intact microsporangia. Ekambaram and Venkatanathan (1933) investigated the species in detail and found that the first two or three leaves that appear during the resumption of growth by the axis are sterile or possess only abortive sporangia. The leaves that arise later are all fertile. They observed two kinds of plant: (***i***) bisporangiate plants and (***ii***) megasporangiate plants. The megasporangiate plants are found in abundance and bear only megasporophylls with megasporangia at their bases. The megasporophylls are arranged in close spirals. In the bisporangiate plants there are only one or two microsporophylls and the rest are all megasporophylls. These plants are less common and were encountered during early rainy season. The ratio of bisporangiate plants to megasporangiate plants is 2 or 3 to 50. There is no external difference between the two kinds of plants. The first microsporophylls, develops after the formation of two or three megasporophylls. In case there are two microsporophylls, the second one does not develop immediately after the first but it comes up later, *i.e.*, after the formation of a few megasporophylls. The megasporophylls that develop late have megasporangia with immature megaspores or do not form megaspores at all. This is probably due to onset of unfavourable conditions.

In ***Isoetes lacustris*** innermost leaves are sterile, the middle ones are microsporophylls and the outermost are megasporophylls. Gluck (1924) studied various species of ***Isoetes*** and observed a number of variations in the arrangement of the microsporophylls and the megasporophylls. His result reveal that there is no regularity in the arrangement of the sporophylls with respect to each other. Wilson Smith (1900) also observed irregularity in their arrangement. West and Takeda (1915) studied in detail the morphology and ontogeny in ***Isoetes japonica***, and found no regular sequence in the development of sporophylls. They are irregularly distributed.

The Velum

It is a characteristic structure that arises below the ligule and develop very early in the history of development of the leaf. It originates from the tissue between the ligule and the sporangium (Fig. 5.7, A—E and 5.11, A). The velum is a lobed structure. The upper lobe or the **labium** grows obliquely upwards and remains short whereas the lower lobe grows downwards and is continuous with tissues of the leaves at the sides. In some species the lower lobe covers the entire sporangium, like a pouch, leaving only a small slit-like aperture below. Such a condition is found in the terrestrial species, ***e.g., Isoetes hystrix***. In aquatic species the velum is not so well developed and the lower lobe only partially covers the sporangium. In ***Isoetes coromandelina*** the lower lobe is completely absent.

Several conflicting accounts regarding the development of velum have appeared. Majority of them describe that velum originates from the upper tiers of cells resulting from the divisions of the sporangium initials. Hofmeister (1862) described that velum separates from the sporangium by the earlier divisions of the sporangial initial. Wilson Smith (1900) regards it as the 'sterilised portion of a sporogenous tissue, or a part of the 'sporangium fundament'. Braun (1863), Scott and Hill (1900) describe that in ***I. hystrix*** velum has an origin from a tissue quite distinct from that of the sporangium. Ekambaram and Venkatanathan (1933) studied the development of velum in ***I. coromandelina*** (Fig. 5.7 and 5.11) and observed that it has an independent origin. They point out that velum originated much earlier than the appearance of sporangial initials. The velum has distinct epidermal layers at its free portion. The tissue between the epidermal layers is made up of large cells that are colourless (Fig. 5.11, A) and lose their contents when mature. Some of these cells develop into tracheidal cells with spiral or annular thickenings (Fig. 5.11, A). Such cells make their appearance first in the upper free portion and later in the lower portion. The tracheidal cells of the velum have a definite connection with the vascular bundle of the leaf by "a narrow strip of tracheidal cells" (Ekambaram and Venkatanathan, 1933). Wilson Smith (1900) denies any such connection in ***I. echinospora*** and ***I. englemanni***. In ***I. coromandelina*** velum was also found to develop on the sterile leaves.

Ekambaram and Venkatanathan (1933) regard it as purely vegetative structure because of the following characteristic features :

1. It originates quite independent of the sporangium.
2. Its formation in sterile leaves.
3. Presence of connections between the vascular tissue of the leaf and the tracheidal cells of the velum.

Sporangia

(*a*) **Position and Structure** (Fig. 5.7, 5.11 to 5.14). In ***Isoetes coromandelina*** the sporangia originate from the group of cells below the velum. They have no ontogenetic connection, whatsoever with the velum. In some species the lower lobe of the velum covers the entire sporangium except near its base. In others the sporangium is only partially covered. In ***I. coromandelina*** the lower lobe of the velum is absent and the sporangium is naked.

The sporangia are sessile and are almost oblong-rounded in shape and vary in length from 4 to 10 mm. They arise at the base of the sporophylls and are, therefore, foliar in nature. They occur singly and are adaxial. The mature sporangium is surrounded by a sterile jacket of three or four layers of cells. The innermost layer is made up of large and transparent cells with distinct nuclei. This is called the **tapetum**. In some species (***I. nuttallii***) the tapetum is two-layered. The cavity of the sporangium is incompletely divided by transverse partitions of sterile tissue called the **trabeculae** (Fig. 5.14). These trabeculae are numerous in megasporangia and comparatively fewer in microsporangia. The incompletely divided sporangial cavity is full of sporogenous tissue which later distinguishes into

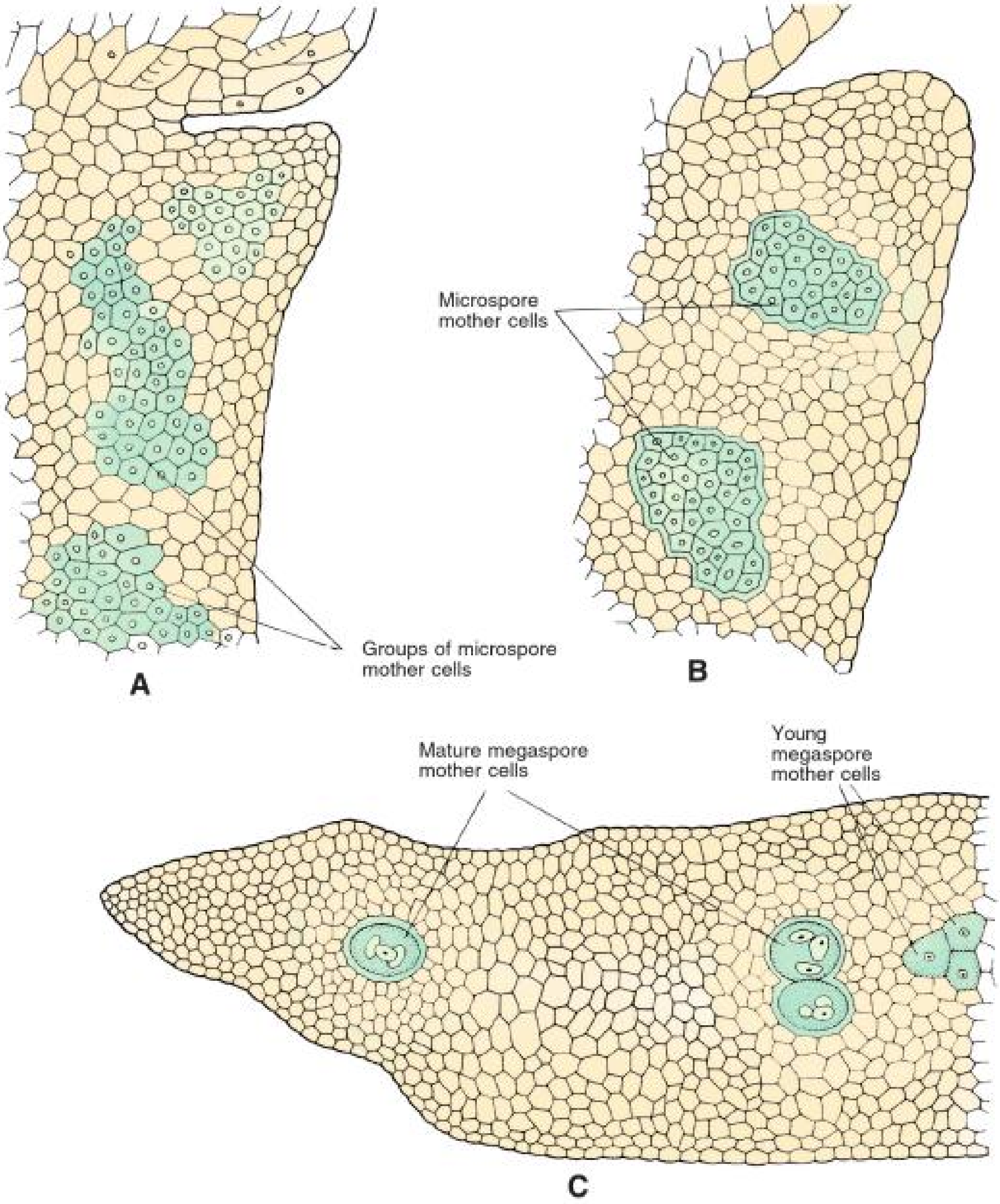

Microspore
mother cells
A
Groups of microspore
mother cells
B
Mature megaspore
mother cells
Young
megaspore
mother cells
C

Fig. 5.12 (A—C). *Isoetes coromandelina.* Stages in the development of sporangia. **A, B.** Earlier stages in the development of a microsporangium. Groups of microspore mother cells are quite distinct; **C.** Early stage in the development of a megasporangium. The wall layers and the trabeculae have not differentiated as yet. (After Ekambaram and Venkatanathan).

spore mother cells or the **sporocytes**. The sporogenous cells adjacent to the trabeculae and sides of the sporangium become modified into tapetal cells. The rest of the sporogenous cells function as potential sporocytes. At this stage the micro and megasporangia follow a different course of development.

The microsporangia contain a large number of microspore mother cells, which undergo meiosis and produce 150,000 to 1,000,000 microspores. The megasporangia contain a limited number of megaspore mother cells usually 40 to 80. The number of megaspores varies between 160—320 per megasporangium.

(*b*) Development (Fig. 5.7, 5.11—5.14). The development of the two kinds of sporangia follows a similar course of events upto the differentiation of fertile sporogenous tissue. Both the kinds of sporangia originate from the uppermost layer of cells of the sporophyll between the velum and the base of the sporophyll (Fig. 5.7, E). This layer of cells divides in all planes to give rise to group of sporangial cells. These cells are similar and undifferentiated. No demarcation between the peripheral jacket cells and central sporogenous cells exists during early stages of development. Periclinal divisions have no doubt, been observed in the outer cells of the undifferentiated mass. These divisions add a large number of cells to the inner mass of cells leading to the formation of a young sporangium composed of a mass of uniform cells (Fig. 5.11, B). In I. ***nuttallii*** (G.M. Smith, 1955) the young sporangium, at this stage, shows a differentiation into a single outermost layer of cells from a large group of central cells (Fig. 5.13). The latter have distinct nuclei and denser cytoplasmic contents and can be regarded as sporogenous cells. No such differentiation (Fig. 5.11, B) has been observed in ***I. coromandelina***.

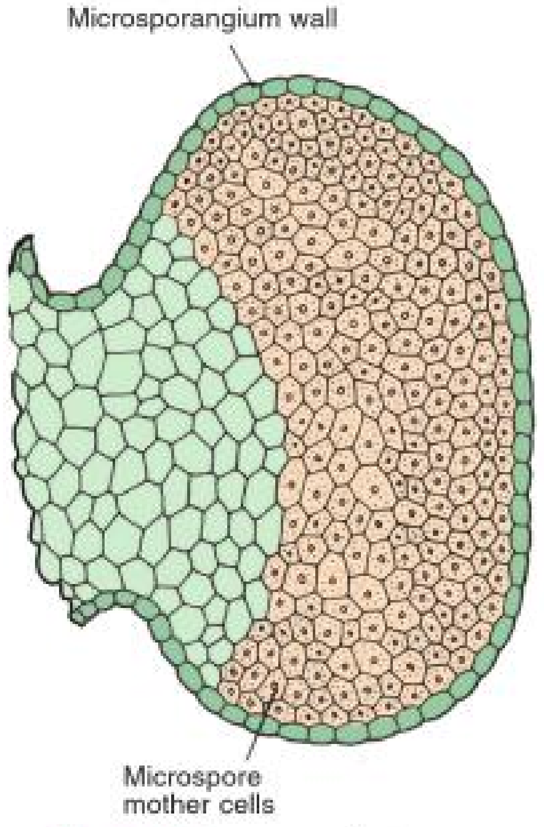


Fig. 5.13. ***Isoetes nuttalli.*** A young microsporangium (After Smith)

The uniform sporangial mass undergoes change after attaining a fairly big size. These changes determine the type of the sporangium and follow a different sequence in the mega and the microsporangia. These will be discussed under two separate headings :

The Megasporangium

In case the sporangial mass is destined to develop into a megasporangium, the following changes take place in it :—

1. Some individual cells or groups of 2 to 3 cells (***I. coromandelina***) enlarge in size. Their nuclei attain large size and the cytoplasmic contents become denser so that they can be easily distinguished from the surrounding cells (Fig. 5.12, C). These cells are the ‘potential megaspore mother cells’.

2. All the potential megaspore mother cells are not capable of reaching maturity. Their differentiation is followed by a considerable enlargement of the sporangium. The megaspore mother cells also enlarge considerably.

3. Some of the megaspore mother cells stop growing. Their contents becomes less dense and vacuolated. Besides this, a number of megaspore mother cells become abortive. These abortive mother cells divide and redivide to form

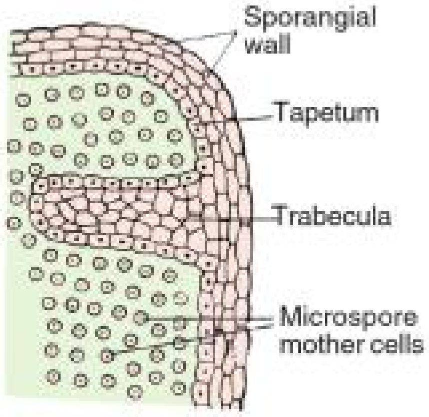


Fig. 5.14. ***Isoetes.*** T.S. microsporangium showing a trabecula, tapetum, microspore mother cells and sporangial wall.

groups of sterile cells. The functional mother cells keep on increasing in size and become rounded or elliptical in shape.

4. After the functional mother cells have reached maturity and are ready to divide and produce spores., there is differentiation of the sterile tissue into tapetum, trabeculae and jacket cells. The outermost three or four layers of sterile cells differentiate into the jacket of the sporangium and the tapetum. The abortive mother cells form strands of sterile cells that become differentiated as trabeculae. The sterile cells around the trabeculae also differentiate into one to two or many layers of tapetum (Fig. 5.14). The tapetal layers around the trabeculae are continuous with the tapetum of the sporangial wall. In ***Isoetes coromandelina*** some sterile cells surrounding the megaspore mother cells degenerate and are completely dissolved to form cavities of the sporangium. After the formation of these cavities the trabecular cells elongate and form distinct trabecular strands.

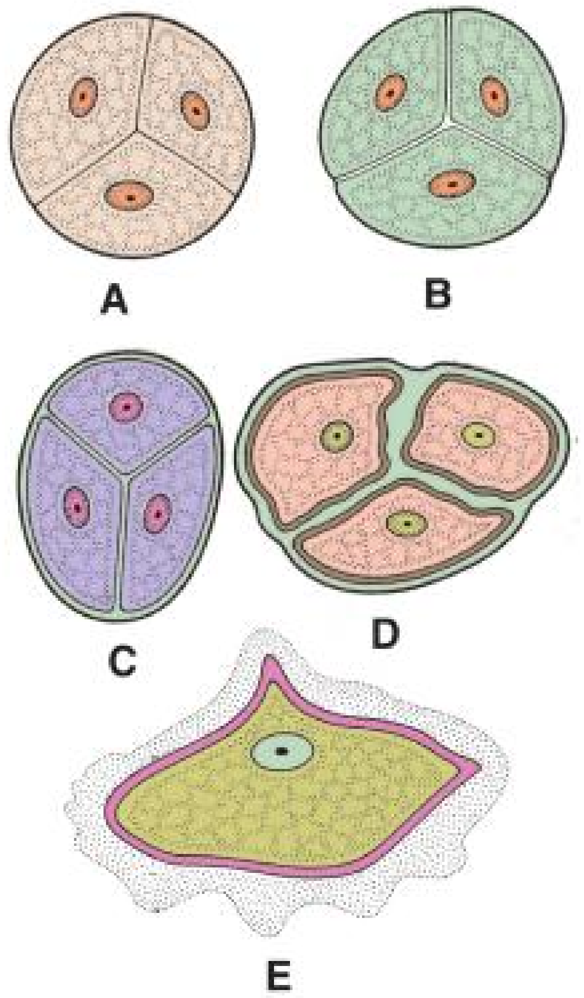


Fig. 5.15 (A-E) ***Isoetes coromandelina.*** Stages in Megasporogenesis. (After Ekabaram and Venkatanathan)

5. The megaspore mother cells undergo meiosis and form tetrads of haploid megaspores. The four haploid nuclei formed as a result of meiosis separate into haploid cells by cytokinesis. Cytokinesis is accomplished by the formation of a fine cell plate between the nuclei (Fig. 5.15, A). Later the cell plate splits (Fig. 5.15, B) thus separating the four cells still enclosed within the parent wall of megaspore mother cells (Fig. 5.15 D). Each of the four daughter cells secretes a wall around itself and contains a plastid body. These cells now grow in size and their cell walls also undergo changes. These cells become thick-walled megaspores. They are arranged in tetrahedral tetrads. As the spores differentiate the plastids disappear. The megaspores wall increase in thickness and is finally differentiated into three layers. The megaspores are now mature. The wall of the megaspore mother cell disappears so that the megaspores lie free in the cavity of the megasporangium.

The Microsporangium

In the microsporangium the sterile sporangial mass differentiates into groups of microspore mother cells and sterile cells (Fig. 5. 12, A, B). All the microspore mother cells are functional and undergo reduction division to give rise to an exceedingly large number of microspores. There is absolutely no degeneration of the microspore mother cells. The sterile cells around the microspore mother cells differentiate into trabeculae. Wall layers and tapetum are formed in the same fashion as in the megasporangium. After the formation of microspores the sterile cells around them lose their contents and ultimately disintegrate so that the microspores lie free in the cavities between the trabeculae.

The microspore mother cells undergo meiosis. After the completion of meiosis, the haploid daughter protoplasts separate, by the formation of cell plates and their resultant splitting (Fig, 5.16). Later they mature into microspores that separate and are set free from the surrounding microspore mother cell wall. At this stage they are more or less semilunar in shape (Fig. 5.16, D, E). Later they become bean-shaped and their cell walls become differentiated into three layers.

Dehiscence of the Sporangia

The sporangia in ***Isoetes*** are indehiscent and the two types of spores are liberated only when the sporophylls decay after the end of the growing season. Osborn (1922) reported that in ***I. drummondii***, that grows in vernal pools, with its axis buried completely in the soil, the spores are exposed or brought above the ground by expansions of mucilage cells at the bases of sporophylls. Ekambaram and Venkatanathan (1933) reported that in ***I. coromandelina*** the spores are liberated by the breaking up or by the decay of the portions of the sporangia attached to the sporophyll base.

Spores are mostly wind disseminated. They are also carried by water in aquatic species. Earthworms have also been reported to carry the spores from place to place.

Structure of the Spores

(a) The megaspores

The megaspores are usually white, grey or black in colour. They are tetrahedral in shape (Fig. 5.15, E) and vary in diameter from 200-900µ. The wall is differentiated into three layers. The outermost layer is usually thick and variously sculptured. In ***I. coromandelina*** it is marked with large tubercles (Fig. 5.15, E). There is a distinct triradiate ridge. The outer wall is called **exosporium**. Next to it is the **mesosporium** which is followed by **intine** or **endosporium**. According to some authors the original cell wall that separates the spore tetrads develops, in each spore into an outermost sculptured layer called the **epispore**. Later exine or exosporium, mesine or mesosporium and entine or endosporium develop. According to them the spore wall is four layered. The spore protoplasm shows a spongy structure and contains food reserves in the form of starch. The nucleus, in the mature spore, lies at its apex (Fig. 5.15, E) or at its base (***I. braunii***). It has no central vacuole and has dense cytoplasmic contents.

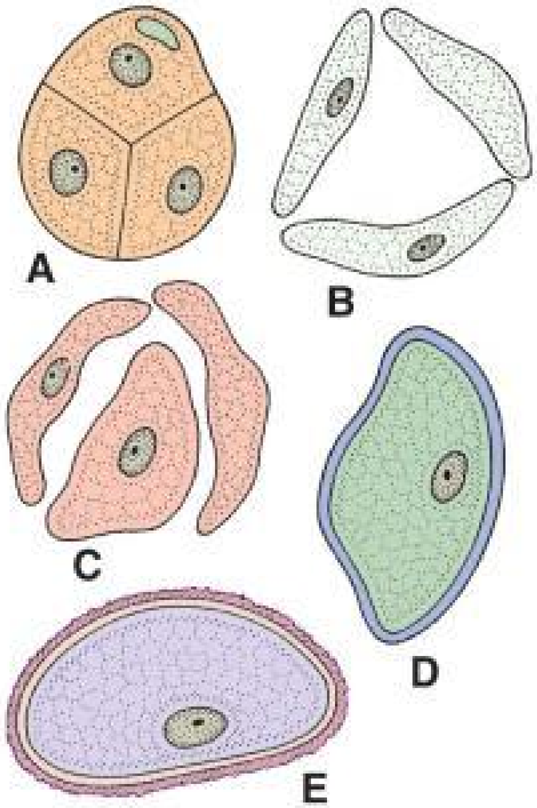
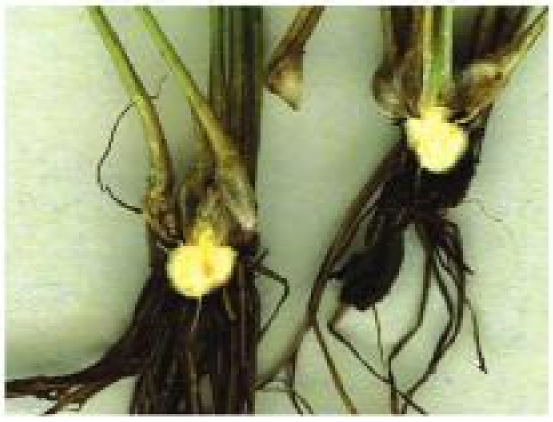


Fig. 5.16 (A-E). Microsporogenesis in *Isoetes coromandelina* (After Ekambaram and Venkatanathan)



I. braunii

(b) The microspores

They are smaller in size and vary from 20—45µ in diameter. The microspores are semilunar in shape when young but become kidney-shaped at maturity. The cytoplasm is thin and finely vacuolated. The nucleus lies on one side. The microspore wall is three layered. The outermost layer or exine is marked with small densely packed spines (Fig. 5.16, E). They are usually ash coloured or brown.

GAMETOPHYTES

Heterospory leads to the formation of two types of gametophytes in ***Isoetes.*** The microspores germinate to give rise to the male or **microgametophytes** and the megaspores to female or **megagametophytes.** Both types of gametophytes are endosporic. The spores may start germinating immediately after their release from the sporangia or the germination may be delayed depending upon the climate conditions. Quite contrary to ***Selaginella*** the spores in ***Isoetes*** start germinating only after their release from the sporangia.

Microgametophyte

The first division of the nucleus results in the formation of a small **prothallial cell** and a large cell that has been interpreted as **antheridial initial** (Fig. 5.17, B). The antheridial cell undergoes a series of successive divisions to cut off **4 wall cells** surrounding a single **central cell** (Fig. 5.17, C—G). The central cell divides twice to form four **spermatocytes** or **sperm mother cells** (Fig. 5.17, H—J). The four wall cells enclosing 4 spermatocytes represent the antheridium. The wall cells remain intact until the microspore wall cracks (Fig. 5.17, N). This generally happens after two weeks of developmental period. The contents of the sperm mother cells metamorphose into multiflagellate spermatozoids (Fig. 5.17, H, L). The microgametophyte of ***Isoetes*** is the most reduced type known among the vascular cryptogams. One gametophyte produces only four spermatozoids.

After the cracking of microspore wall the exposed wall cells of the antheridium degenerate thus liberating the ***spermatozoids.*** The prothallial cell also degenerates. The multiflagellate sperms of ***Isoetes*** are in striking contrast to biflagellate sperms of other lycopods (***Selaginella***, ***Lycopodium***).

The spermatozoid of ***Isoetes*** (Fig. 5.18) has been described by Dracinshi (1932). The free swimming spermatozoid consists of two large and spherial vesicles (Fig. 5.18). The vesicles are soon lost. Each vesicle contains fat and vacuole elements. Starch is considered to be absent. The nucleus pointed at either end is enclosed within a spongy plasmatic structure. The nucleus does not extend to the pointed anterior end of spermatozoid. The

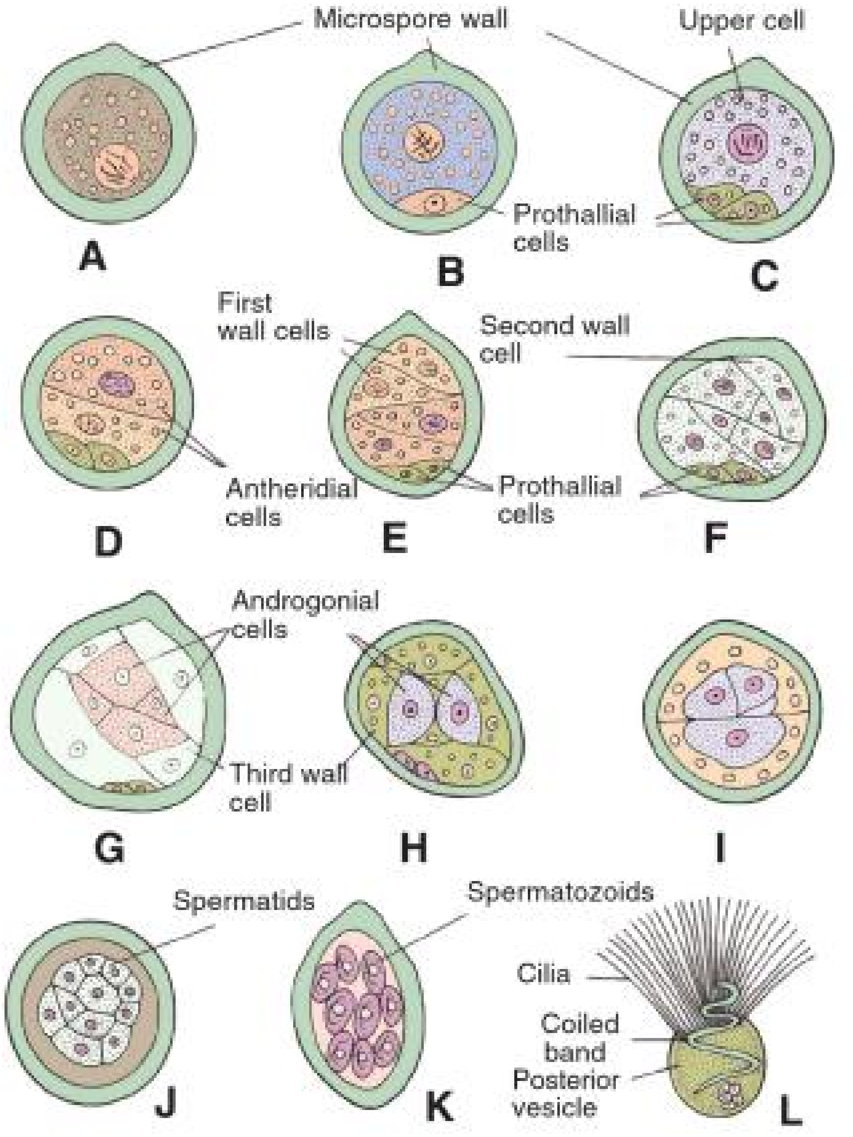


Fig. 5.17 (A-L). *Isoetes lacustris.* Various stages in microspore germination and formation of male gametophyte. For explanation see text (After Liebig)

flagella bearing band or the stalk is homogeneous and bears about 25 flagella. The flagella arise from the **basal granules** situated on the stalk. Four basal granules are grouped together at the anterior end whereas the rest are scattered in a single row along the stalk.

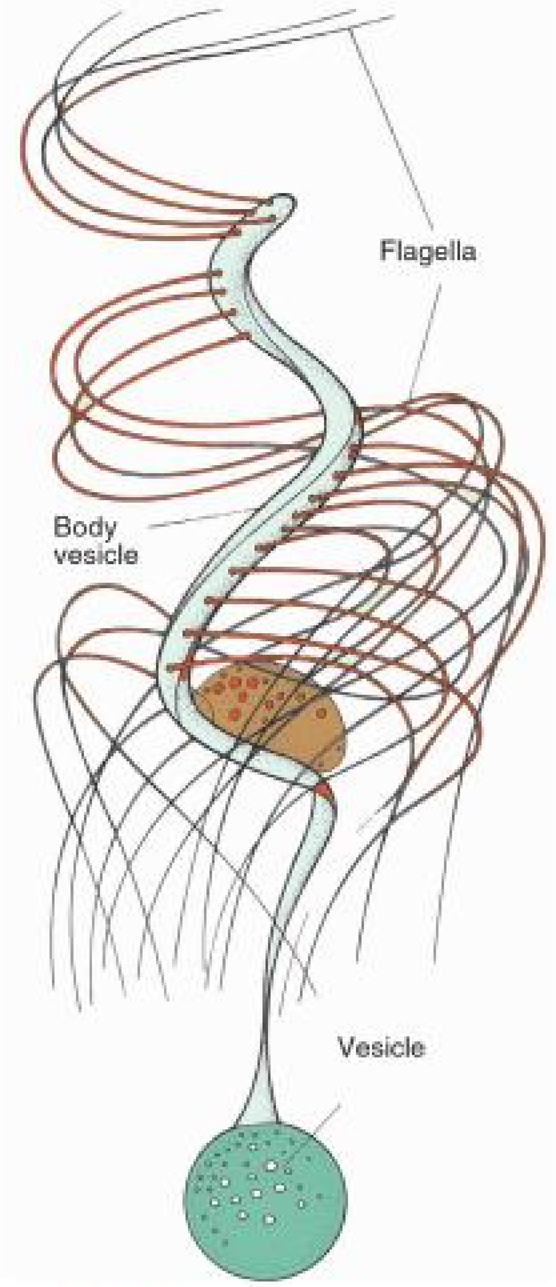


Fig. 5.18. Spermatozoid of *Isoetes.*

Megagametophyte (Fig. 5.19, A—D)

The nucleus of the tetrahedral megaspore divides by free nuclear divisions until 30—50 free nuclei are formed. The nuclei migrate through the cytoplasm and get distributed along the periphery of the spore protoplast. The larger number is near the apex (triradiate ridge). Wall formation starts after 30—50 free nucleate stage. The nuclei at the apical portion of the spore are quite close to each other and are the first to be surrounded by walls. From here wall formation extends basipetally and then towards the centre at a comparatively slower rate. The whole megaspore is ultimately filled with cells. The cells at the apex are smaller in size and contain reserve food material. There is no diaphragm demarcating the upper small-celled and lower large-celled tissue. This cellular tissue is the female gametophyte and is surrounded by the megaspore wall, which later cracks along the triradiate ridge thus exposing the upper small-celled tissue. The exposed part does not protrude out as in ***Selaginella***. A number of rhizoids develop from the exposed part. Archegonia develop in the exposed small-celled tissue. The first archegonium appears at the apex and is thus median in position (Fig. 5.19, A). The number of archegonia varies from 3—20 or 30 in some species. The number of archegonia in a female prothallus depends upon fertilization. In case the first archegonium is fertilized the others may not develop at all. Their formation stops after fertilization. In case fertilization is delayed the archegonia go on developing till the entire food supply is exhausted.

Archegonia

The archegonia are sunk in the tissue of the female gametophyte and only the upper tier of neck cells may protrude out slightly. Each archegonium (Fig. 5.19, D) consists of a neck made up of 4 longitudinal rows of 4 cells each, a single **neck canal cell.** The venter has a **ventral canal cell** and **egg**. Being embedded the venter has no sterile jacket. At maturity the neck canal cell and ventral canal cell distintegrate and push apart the neck cells thus making an open channel for the spermatozoids to enter (Fig. 5.19, E).

The archegonium develops (Fig. 5.19, A—E) from a single superficial cell which divides periclinally into an upper and a lower cells. The outer cell divides anticlinally/periclinally to form four tiers of four cells constituting the neck. The lower divides periclinally to form a **neck canal cell** and a **primary ventral cell.** The latter divides into a **ventral canal cell** and **an egg cell**.

Fertilisation has not been observed in ***Isoetes*** but it takes place.

The Embryo

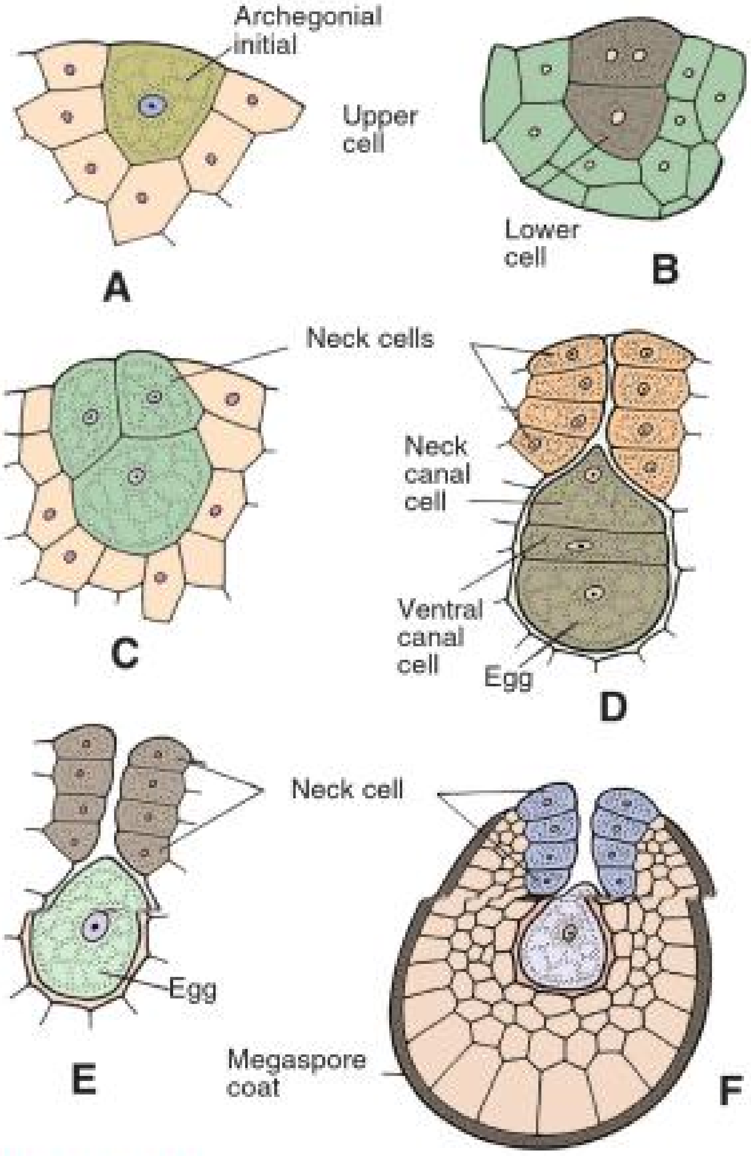


Fig. 5.19 (A-F). *Isoetes echinospora.* A-D Stages in the development of an archegonium; E. A mature archegonium; F. Mature archegonium enclosed in female gametophyte. Megaspore wall is also shown.

The fertilized egg in ***Isoetes*** almost fills the cavity of the venter. The fertilised egg divides by a transverse or oblique transverse wall (Fig. 5.20, B). Both the cells take part in the formation of the embryo and no suspensor is formed. The cell towards the neck of the archegonium can be regarded as the **hypobasal cell** and the one away from the neck as the **epibasal cell**. The next two divisions are at right angles to the first wall and to each other thus forming an **octant stage.**. The hypobasal tier gives rise to the foot alone. The epibasal tier gives rise to the first leaf and the root and also the shoot apex after some delay. Due to the absence of suspensor the development of embryo is **exoscopic**, but further developmental changes suggest it to be **endoscopic.** The octant stage by further development forms an oviod mass of undifferentiated cells. Later division lead to the widening of the embryo in the plane of the basal wall (Fig. 5.20, D). Later the first leaf originates from one half of the epibasal region (Fig. 5.20, D). From the base of the first leaf a large cell becomes prominent and divides first by periclinal walls to distinguish a ligule. A semicircular ridge appears at the same time at the base of the root. This is the primordium of the **velum**. Between the base of the velum and the first leaf there is a small cleft. In this cleft there distinguishes a small group of cells. This group of meristematic cells is destined to give rise to the shoot apex at a later stage. The second leaf develops facing the first with the shoot apex lying between them. Campbell (1918, 1939) observed that the vascular strands of the first leaf and the first root coincide with each other. The foot is small in young embryo but it becomes massive and well developed in mature embryos. During its growth, the embryo elongates downwards and erodes the prothallial tissue. The uneven growth of the embryo makes it curved and as this growth continues, accompanied by rapid absorption of prothallial tissue, the polarity of the embryo becomes reverse. The foot which in the young embryo is towards the archegonial neck, comes to lie on the lower side (Fig. 5.20, D) and the long axis of the embryo lies parallel to the

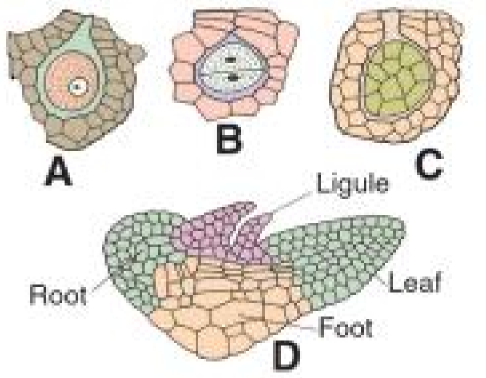


Fig. 5.20 (A-D). *Isoetes echinospora.* Stages in the development of embryo. (After Campbell)

surface of the prothallus (Fig. 5.20, D). The young leaf elongates rapidly and in a horizontal direction. It comes out of the prothallus in horizontal position and later turns up. The root curves downwards and as the sporophyte grows it straightens out and all its traces of horizontal position are lost. The foot develops and persists till the storage tissue of the gametophyte lasts. It perishes after the young sporophyte becomes independent. The first leaf bursts out of the prothallus after seven days of the growth of the embryo.

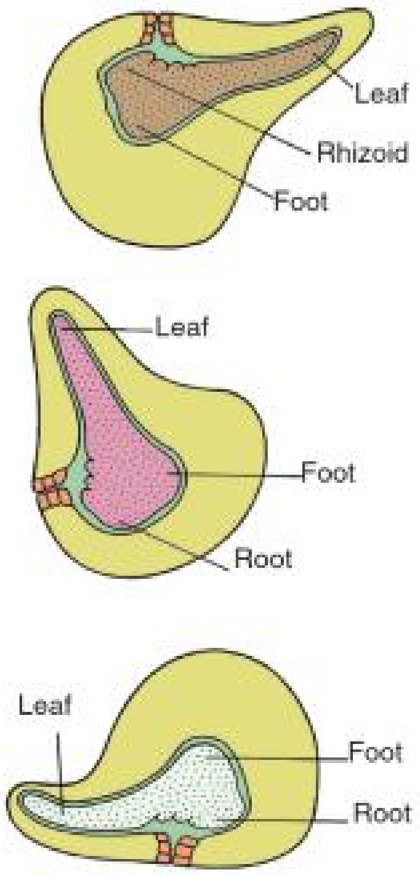

Leaf
Rhizoid
Foot
Leaf
Foot
Root
Leaf
Foot
Root

Fig. 5.21. Embryogeny in differently oriented gametophytes of *Isoetes* (After La Motte).

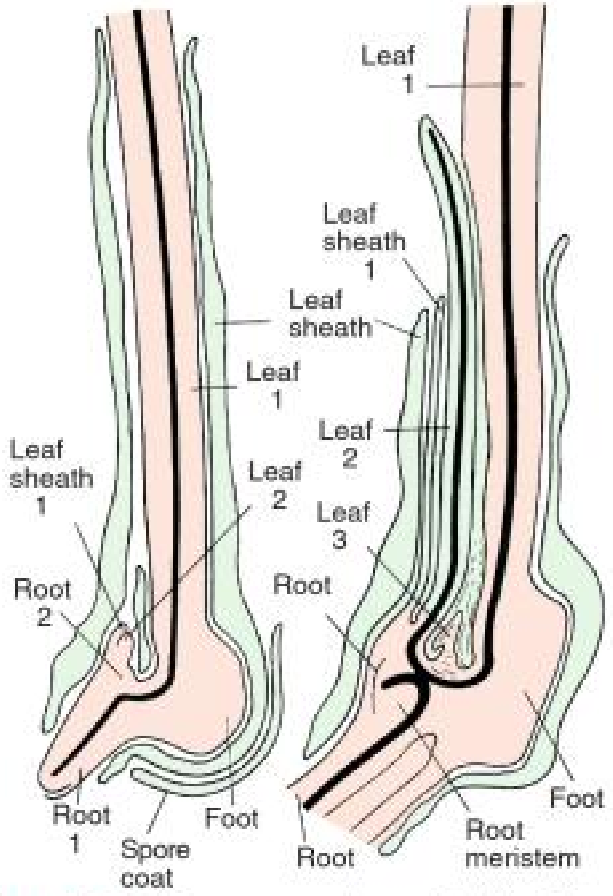

Leaf 1
Leaf sheath 1
Leaf sheath
Leaf 1
Leaf 2
Leaf sheath 1
Leaf 2
Leaf 3
Root 2
Root
Root 1
Spore coat
Foot
Root
Root meristem
Foot

Fig. 5.22. *Isoetes englemanni* (A—B). L.S. Young sporophyte (After Baldwin)

Taxonomic Position

Division	:	***Lycophyta***
Class	:	***Ligulopsida***
Order	:	***Isoetales***
Family	:	***Isoetaceae***
Genus	:	***Isoetes***

Systematic Position

Bower and many other investigators regard ***Isoetes*** as a member of the ligulate Lycopsida because:

1. It has ligulate and microphyllous leaves. The ligule arises in a definite pit (ligule pit).
2. It is heterosporous.
3. The gametophytes are reduced.
4. Germination of spores is similar to ***Selaginella.***
5. Structure of male and female prothalli is also similar to ***Selaginella.***
6. The sporangia are massive and elongate.
7. The arrangement of roots in definite rows is similar to some extinct lycopods like ***Nathorstiana.***
8. There is a very close correspondence in root structure with other lycopods.

Cambell (1939) included it under the eusporangiate ferns because of the following features :

1. Early leaf and root formation.
2. Delayed shoot formation.
3. Relationship of vascular strands of root and leaf.

These features bring ***Isoetes*** closer to ***Botrychium virginianum*** and to some Marattiaceae.

The present consensus of opinion regards ***Isoetes*** as a greatly reduced and highly specialised ligulate lycopod. Some researchers regard the whole plant as single strobilus with roots arising from its base and other reduced vegetative parts telescoped with it. A definite evolutionary sequence leading to the reduced plant body of ***Isoetes*** and ***Stylites*** can be visualised if we insert ***Pleuromia*** and ***Nathorstiana*** as intermediate forms between tree-like extinct ***Lepidodendrons*** and the ***Isoetales*** (Magdefrau, 1932). The reduction series may thus be summarised as :

Lepidodendrales → Pleuromeiopsis → Nathorstianella → Nathorstiana → Pleuromeia → Stylites → Isoetes

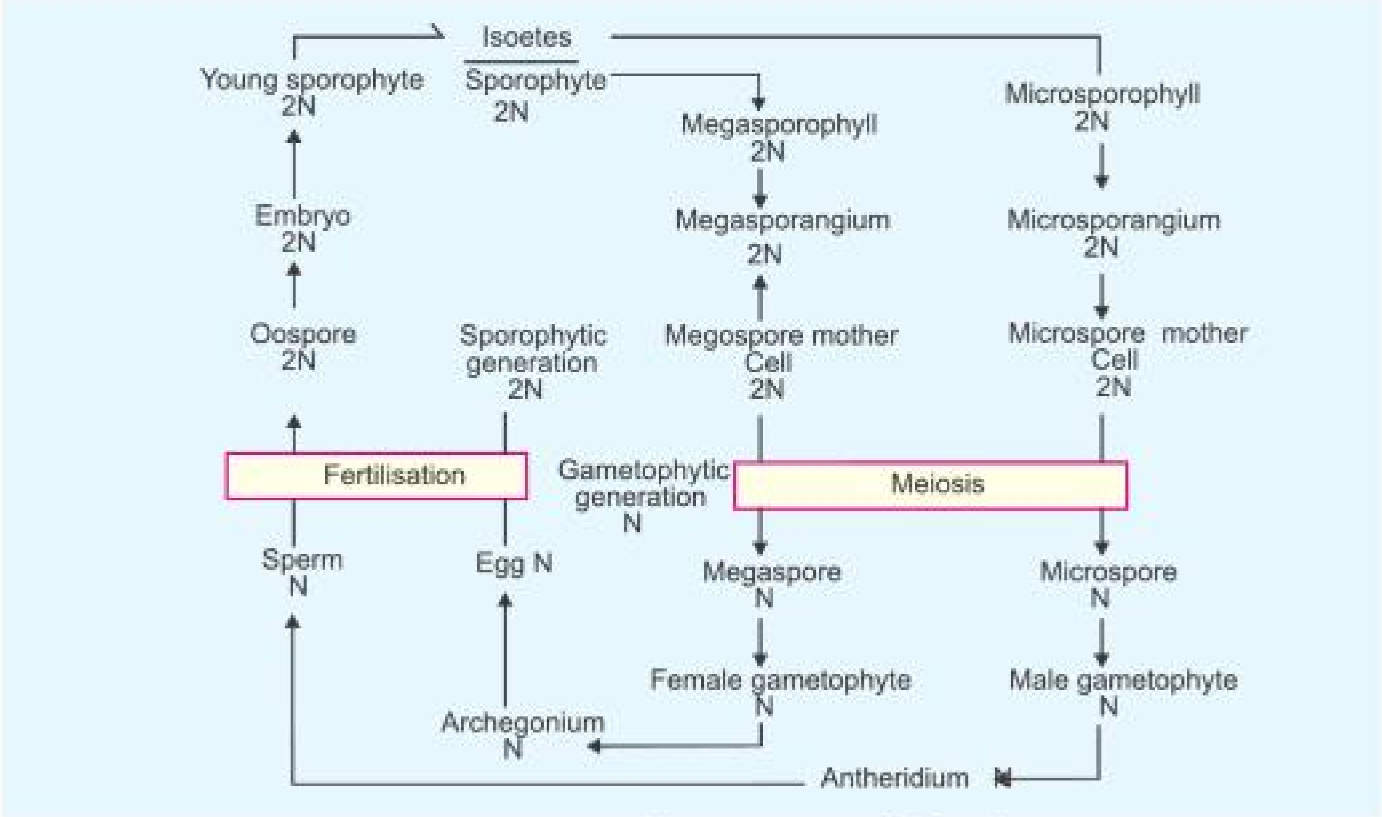

Isoetes
Young sporophyte 2N
Sporophyte 2N
Megasporophyll 2N
Microsporophyll 2N
Embryo 2N
Megasporangium 2N
Microsporangium 2N
Oospore 2N
Sporophytic generation 2N
Megospore mother Cell 2N
Microspore mother Cell 2N
Fertilisation
Gametophytic generation N
Meiosis
Sperm N
Egg N
Megaspore N
Microspore N
Female gametophyte N
Male gametophyte N
Archegonium N
Antheridium

Fig. 5.23. *Isoetes.* Graphic representation of life cycle

Stylites

The other genus of Isoetales is ***Stylites***. The genus was discovered by Amstutz in 1957 from high Andes of Peru. Two species ***Stylites andicola*** and ***S. gemmifera*** have been described. The species generally grow around the boggy margins of a lake at an altitude of 4750 meters. The genus closely resembles ***Isoetes*** but differs in certain respects. The differences have been described below.

Stylites andicola

S. gemmifera

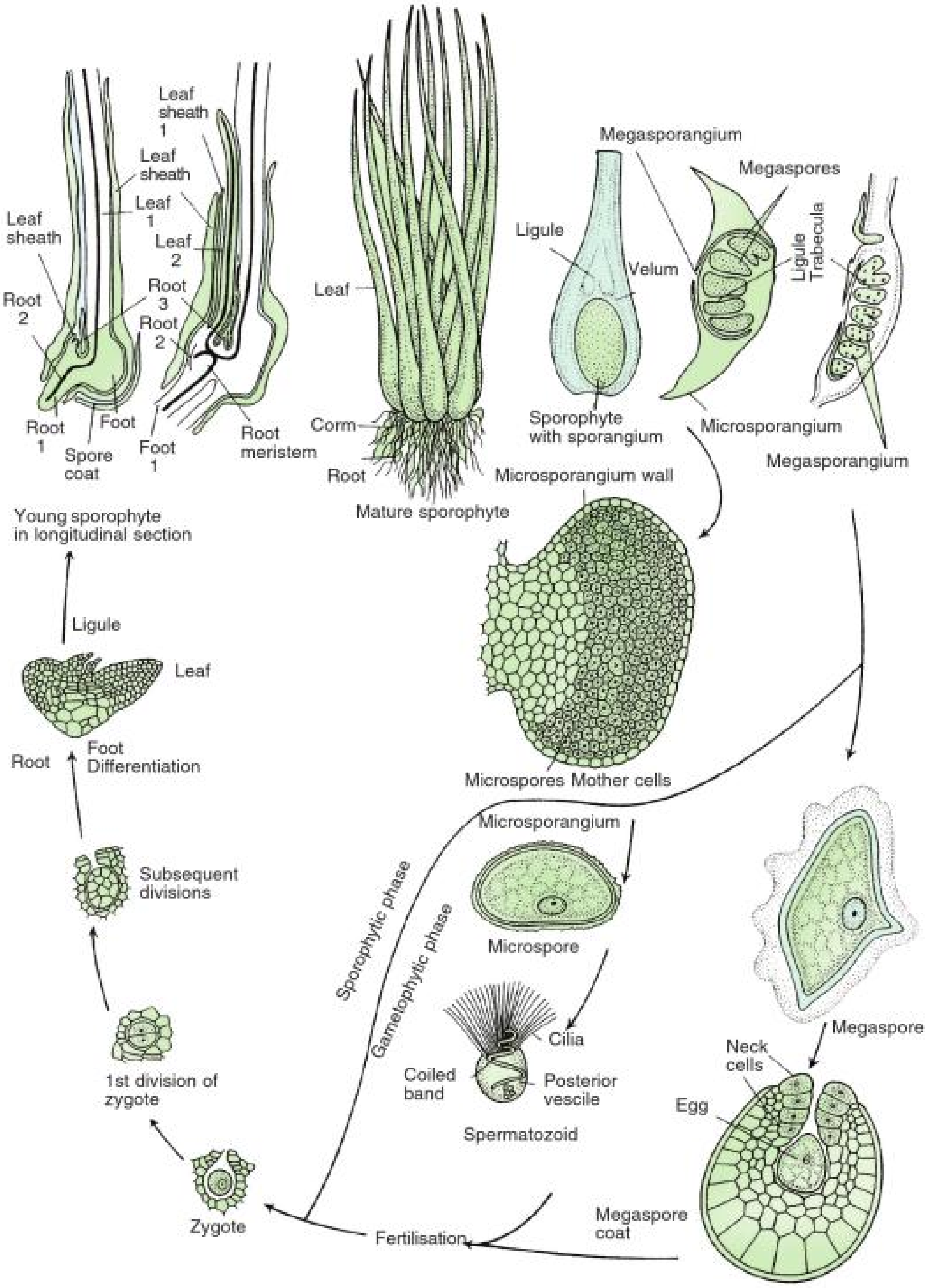

Leaf sheath 1
Leaf sheath
Leaf 1
Leaf sheath
Leaf 2
Root 2
Root 3
Root 2
Root 1
Foot
Spore coat
Foot 1
Root meristem
Young sporophyte in longitudinal section
Leaf
Corm
Root
Mature sporophyte
Megasporangium
Megaspores
Ligule
Velum
Ligule
Trabecula
Sporophyte with sporangium
Microsporangium
Megasporangium
Microsporangium wall
Microspores Mother cells
Ligule
Leaf
Root
Foot
Differentiation
Subsequent divisions
1st division of zygote
Zygote
Sporophytic phase
Gametophytic phase
Microsporangium
Microspore
Cilia
Coiled band
Posterior vescile
Spermatozoid
Megaspore
Neck cells
Egg
Megaspore coat
Fertilisation

Fig. 5.24 : *Isoetes.* Pictorial Life cycle

Isoetes	*Stylites*
1. Small, herbaceous and perennial, plant body consists of a short fleshy upright corm like axis unbranched.	Larger, perennial, the axis is several inches long cylindrical with limited power of vertical growth; axis bifurcates at the crown; dichotomously branched, at least three times to form characteristic tussocks.
2. Roots are mostly unbranched but if branched, it is dichotomous.	Roots are borne in a single deep vertical groove on one side of the lower half of axis. The number of grooves may vary from 1– 3.
3. Leaf : Leaf has a thickened and expanded colourless base and a tapering distal portion which is oval-shaped and pointed.	Similar to *Isoetes*.
4. Vegetative Reproduction : Rare	Common by means of small adventitious buds.
5. Stele : Cylindrial upper part with anchor shaped arm.	Cylindrical upper part with 1– 3 ridges along the xylem cylinder from which root traces aries.
6. Secondary growth – Common and active.	Common but less active.
7. Sporangium – Situated on the adaxial surface mean the expanded base of sporophyll.	Sporangium situated on the adaxial surface far above the sporophyte.

However, the creation of ***Stylites*** has been questioned. According to Rubitzki and Borchert (1964) genus ***Stylites*** has many similarities with ***I. triquetra*** described from Andes of Columbia. It is assumed that ***Stylites*** can be derived from ***Isoetes*** (Bierhorst, 1971) by only contracting the lobes of anchor shaped stele and extending the root producing meristem vertically. Osmund and Raven (1983) reported that ***Stylites*** lacks stomata and absorbs carbon dioxide through roots. In conclusion it may be said that ***Stylites*** is a divergent form of ***Isoetes.***

QUESTIONS

ESSAY TYPE

1. Describe briefly the formation and nature of secondary tissues in ***Isoetes***.
2. Describe in detail the salient features, and classification of Isoetales with special reference to morphological nature of axis and anatomy of sporophyte of ***Isoetes***.
   (Awadh, M. Sc., 2001)
3. Give an account of the important features of order isoetales and discuss its affinities.
   (Kanpur M. Sc., 2000)
4. Describe briefly the distinguishing features of Isoetales. What do you know about the distribution of ***Isoetes*** in India.
5. Describe the life-history of ***Isoetes*** pointing out the features of special interest.
6. Describe the structure of Rhizome of ***Isoetes***. How does it differ from that of ***Lycopodium***.
7. Give a brief account of the axis of ***Isoetes*** and discuss its morphological nature.
8. Describe the structure of sporophyte ***of Isoetes***. How does it differ from that of ***Selaginella***?
9. Give an account of reproduction in ***Isoetes***.

SHORT ANSWER TYPE

10. How would you differentiate between
    (*i*) ***Isoetes*** and ***Stylites***,
    (*ii*) Spore producing organs in ***Isoetes*** and ***Phylloglossum***.
    (*iii*) Spore producing organs of ***Isoetes*** and ***Selaginella***.
11. Give a brief account of sporophyte of ***Isoetes***.
12. Give the characteristic features of ***Isoetes***.
    (Awadh, M.Sc. 2000)
13. ***Isoetes*** shows secondary growth. Discuss.
14. Write short notes on.
    (*a*) ***Isoetes***, **(Rohilkhand M.Sc. 2000)**

(*b*) Axis in ***Isoetes***,

(*c*) Velum,

(*d*) Leaf and ligule,

(*e*) Microspore in ***Isoetes***,

(*f*) Megaspore in ***Isoetes***.

15. Give a brief account of the structure and position of sporangia in ***Isoetes***.

16. Draw labelled sketches of the following:

(*a*) Anatomy of leaf in ***Isoetes***,

(*b*) Microsporangium of ***Isoetes***,

(*c*) Megasporangium of ***Isoetes***,

(*d*) Megaspore and microspore of ***Isoetes***.

17. Briefly describe the development of embryo in ***Isoetes***.

OBJECTIVE TYPE

18. Select the correct answer:

(*i*) Which of the following is commonly called as ***Quillwort*** ?

(*a*) ***Psilotum***

(*b*) ***Lycopodium***

(*c*) ***Selaginella***

(*d*) ***Isoetes***.

(*ii*) The most common species of ***Isoetes*** is

(*a*) ***I. indica***

(*b*) ***I. coromandelina***

(*c*) ***I. mirzapurense***

(*d*) ***I. dixetei***.

(*iii*) Which of the following is the other member of the ***Isoetales*** besides ***Isoetes***?

(*a*) ***Lycopodium***

(*b*) ***Stylites***

(*c*) ***Selaginella***

(*d*) ***Psilotum***.

(*iv*) ***Isoetes*** is

(*a*) ***unisporous***

(*b*) ***Bisporous***

(*c*) ***Homosporous***

(*d*) ***Heterosporous***.

(*v*) Velum in ***Isoetes*** arises

(*a*) above the ligule

(*b*) below the ligule

(*c*) between the ligule and axis

(*d*) as an extension of ligule.

(*vi*) At maturity the microspore of ***Isoetes*** is

(*a*) Oval

(*b*) Circular

(*c*) Kidney shaped

(*d*) Globular.

(*vii*) Sperms in ***Isoetes*** are uninucleate and

(*a*) Uniflagellate

(*b*) biflagellate

(*c*) multiflagellate

(*d*) aflagellate.

Selaginella rupestris
–Erect Habit

CHAPTER 6

Lycophyta — Ligulopsida (Contd.)

- Order Selaginallales
- Description of ***Selaginella*** Palisto-de Beauvios
- Heterospory
- Heterospory and Seed Habit

SELAGINELLALES

The order is represented by single living genus ***Selaginella*** included in the family **Selaginellaceae**. An extinct genus ***Selaginellites*** was discovered from the Carboniferous. It is represented by ***Selaginellites crassicinctus***, ***S. canonbiensis, S. sussei, S. polaris, S. elongatus*** and ***S. primaevae.***

SELAGINELLA Palisto-de Beauvois

Distribution

It is widely distributed genus with 700 species found under diverse climatic conditions. Majority of the species grow under shady and damp places especially in the tropical regions of the world. They are rare in the temperate regions and almost absent in the alpine zone. Some are xerophytic (S. ***lepidophylla***). ***S. oregana*** is epiphytic. Some are cultivated as ornamentals due to their delicate and feathery fronds (***S. picta, S. pygmea, S. kraussiana***).

Seventy-one species of ***Selaginella*** grow in the tropical and subtropical forests along the Himalayas and in the plains of India. Some xerophytic Indian species include ***S. wightii***, ***S. repanda***, etc. Majority of the species grow in the Eastern Himalayas (***S. biformis***, ***S. adunca***, ***S. monospora***, ***S. caulescens*** ; ***S. ciliaris***, ***S. aitchtsoni***, ***S. sanguinolenta***, ***S. jacquemonthi***, ***S. atroviridis***, ***S. nepalensis*** etc.) and comparatively few in the North-Western Himalayas (***S. chrysocaulos***, ***S. chrysorrhizos***, ***S. subdiaphana***, ***S. adunca***, ***S. sanguinolenta***, ***S. pellidissima***, etc.). ***S. exigua***, ***S. ciliaris***, ***S. bryopteris***, ***S. radicata*** and ***S. rupestris*** grow in Pachmarhi hills (central India). ***S. rodrigaesiana*** has been reported from Malabar (Panigrhi, 1978). ***Selaginella involvens***, ***S. radicata*** and ***S. catarctarum*** have been reported from Kodaikanal. Some species also grow in the upper Gangetic plains ***e.g.*** ***S. bryopteris***, ***S. adunca***, ***S. subdiaphana*** and ***S. chrisocaulos***. Some other species that have been reported from eastern India include ***S. willdenovii***, ***S. minutifolia***, ***S. pubescens*** and ***S. wallichii*** (Panigrahi and Dixit, 1966-1968). Haines (1924) reported eleven species from Bihar and Orissa. A number of them grow in U. P. **S. *hallei*** and ***S. amesiana*** are the extinct species reported from Sweden and Illinois.

S. ciliaris

S. pubescens

S. sanguinolenta

Selaginella subdiaphana

MORPHOLOGY OF THE SPOROPHYTE

Habit

Many species of ***Selaginella*** are herbaceous perennials, a few are annuals, ***e.g. S. pygmaea.*** Majority are dorsiventral and grow prostrate (***S. chrysocaulos, S. chrysorrhizos, S. pellidissima, S. kraussiana,*** etc.), a few are radial and grow erect (***S. selaginoides***—Fig. 6.2, A, ***S. rupestris***, etc.), rarely scandent (***S. wildenovii***, ***S. adunca***) and suberect. Some dorsiventral species are **caulescent** with erect stems arising from creeping rhizomes (***S. umbrosa***). They range in size from a few centimetres (***S. pygmaea***) to a few metres (***S. pentagona***) in length and are capable of

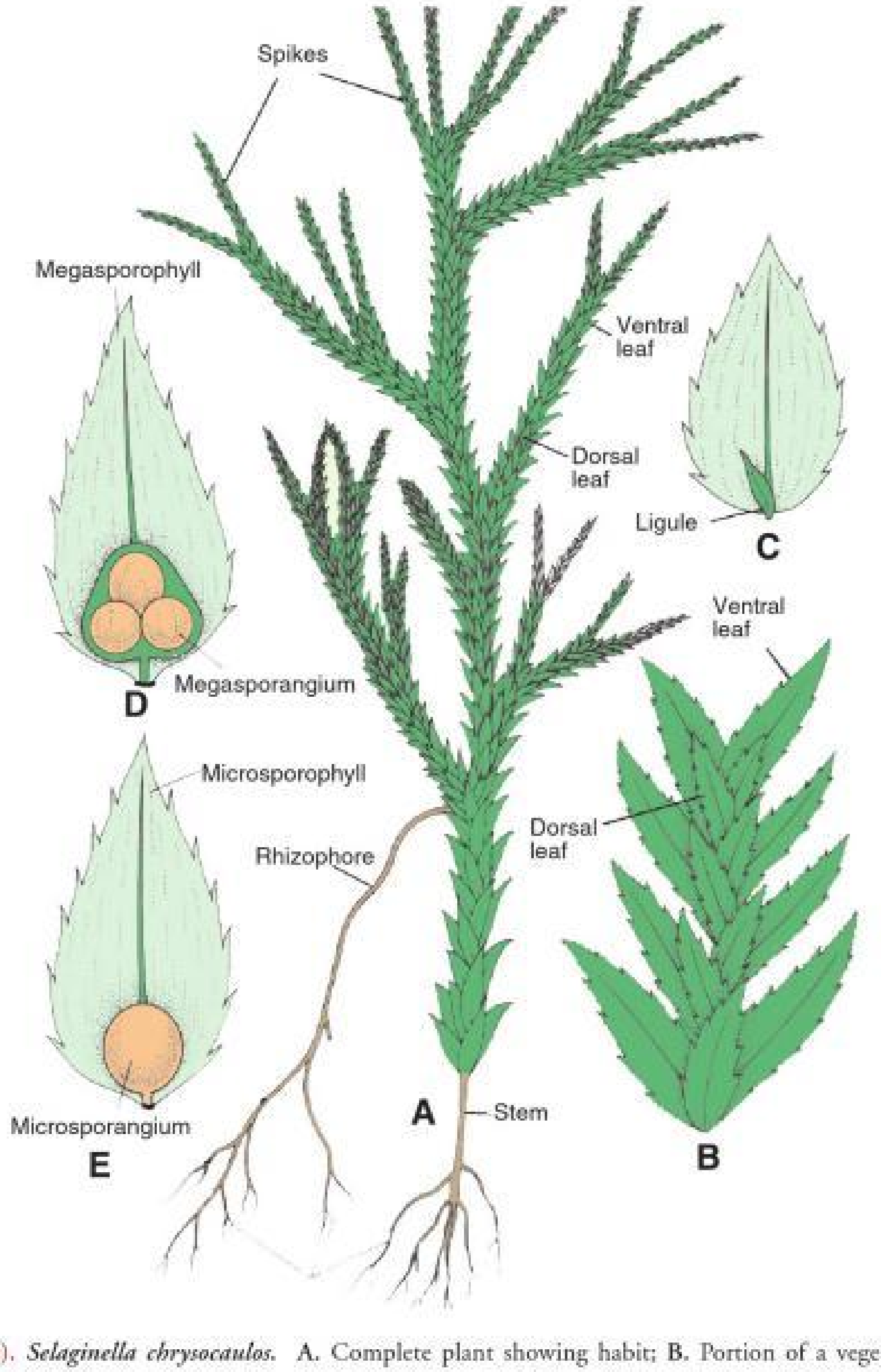

Spikes
Megasporophyll
Ventral leaf
Dorsal leaf
Ligule
C
Ventral leaf
Megasporangium
D
Microsporophyll
Rhizophore
Dorsal leaf
Microsporangium
E
A
Stem
B

Fig. 6.1 (A—E). *Selaginella chrysocaulos.* **A.** Complete plant showing habit; **B.** Portion of a vegetative shoot showing leaf arrangement; **C.** A leaf with a ligule; **D.** A megasporophyll bearing a megasporangium; **E.** A microsporophyll bearing a microsporangium.

growing through and over the bushes (***S. wildenovi***). ***S. viridangula*** grows erect and is several feet tall. ***S. alligans*** is a climber and does so with the help of rhizophores that develop pad-like discs at their ends and attains a length of upto 2 to 8 metres. Some unbranched species are also known. The xerophytic species dry up and curl-like balls during dry seasons and again expand during favourable season or on wetting with water.

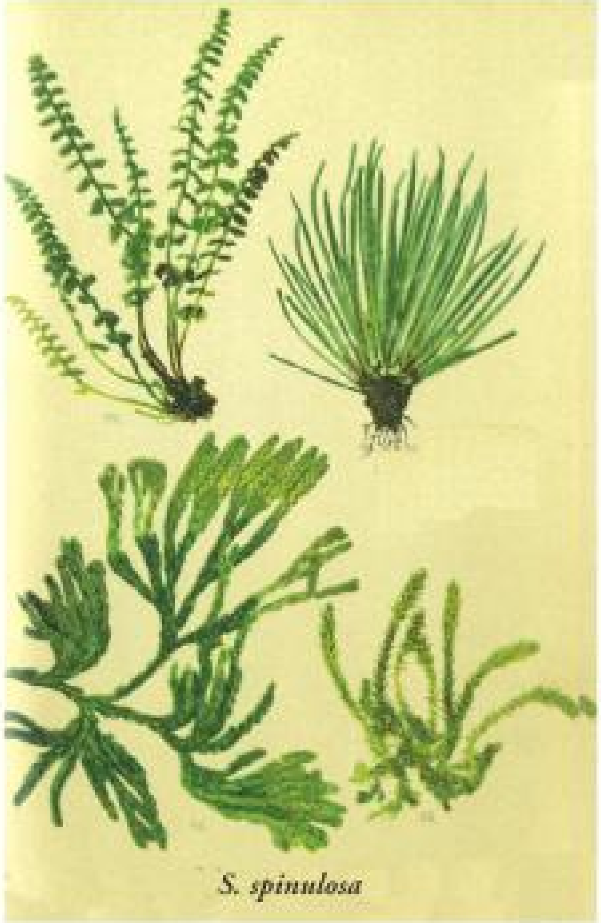
Hieronymus (1902) divided the genus into two sections:

1. Homoeophyllum

This section includes about fifty species all of which have uniform or isophyllous leaves that are spirally arranged. They are all monostelic. This section is further divided into two sub-sections :

(*a*) Sub-section **: Cylindrostachya :** It includes those isophyllous species in which the sporophylls are spirally arranged (Fig. 6.2, A) ***e.g.***, ***S. selaginoides***, ***S. spinosa***, ***S. spinulosa*** etc.

(*b*) Sub-section **: Tetragonostachya :** Species included in this section are isophyllous but the sporophylls are arranged in 4 vertical rows and give the strobilus a four-angled appearance ***e.g.***, ***S. pygmaea***, ***S. uliginosa***, ***S. rupestris***, ***S. oregana***, ***etc.***



S. spinulosa

2. Heterophyllum

This section includes large number of species that are characterised by dorsiventral symmetry and by anisophylly (two kinds of leaves). The leaves are arranged in four longitudinal rows along the stem. There are two rows of smaller leaves attached to the upper side of stem and two rows of larger leaves attached laterally. The strobili are tetragenous (four-angled) and may be isophyllous or anisophyllous. The section is further sub-divided into two sub-sections ***e.g.***, **Pleiomacrosporangiate** and **Oligomacrosporangiate,** on the number of megasporophylls in the cone. The common species included in this section are ***S. chrysorrhizos***, ***S. martensii***, ***S. kraussiana*** etc.

Stem

The stem is herbaceous, branched (rarely unbranched), solid, and may be prostrate, sub-erect, caulescent, climbing or erect. The erect species (***S. selaginoides***, ***S. rupestris***, ***S. pygmaea***) are radially constructed and belong to the section **Homoeophyllum.** The rest are all dorsiventral and are included under the section **Heterophyllum** (***S. chrysocaulos***, ***S. chrysorrhizos***, ***S. pallidissima***, ***S. krussiana***, etc.). Stem is usually green, smooth and glabrous, but it may be coloured red (***S. umbrosa***, ***S. haematoides***) and bear unicellular hair (***S. braunii, S. vogelii***). It is also articulated in some North American species.

Bruchmann investigated ***S. selaginoides***. The young sporophytes of this species consist of a hypocotyl (Fig. 6.2, A) that continues downwards into a primary root and upwards it bears two cotyledons that surround the shoot apex. Later, pairs of **epicotylar leaves** make their appearance. After this the first stem develops and divides dichotomously into two equal limbs that bear spirally arranged isophyllous leaves. The two limbs of the first dichotomy again branch dichotomously and ultimately monopodially (Fig. 6.2, A). The monopodial lateral branches arise in one plane and are at right angles to the first dichotomy thus giving the entire shoot a fan-like appearanace. Strobili develop at the tips of stronger branches, whereas the rest remain sterile. The main axis and the hypocotyl remain as permanent structures (Fig. 6.2, A). The lower base of the hypocotyl swells up and gives out roots.

In the common and widely distributed ***S. chrysocaulos*** the prostrate and dorsiventral stem (Fig. 6.1, A) is repeatedly branched. The branching appears to be dichotomous in the younger portions of the stem and monopodial or lateral in the older portions. Smith, Scot and others hold that all the branches are really lateral but they appear to be dichotomous because they are formed so near the growing apex that the latter seems to give rise to two equal shoots. These shoots in the early formed portions of the plant grow with equal vigour so that it becomes difficult to distinguish between the main axis and the lateral branch. The equal growth of the main axis and the branch give the appearance of a dichotomy. The difference between the main axis and the branches becomes evident in later formed parts of the plant where the main axis grows vigorously and the branches remain small. Eames, Schoute, and others hold that branching in dorsiventral species of ***Selaginella*** is dichotomous or pseudomonopodial.

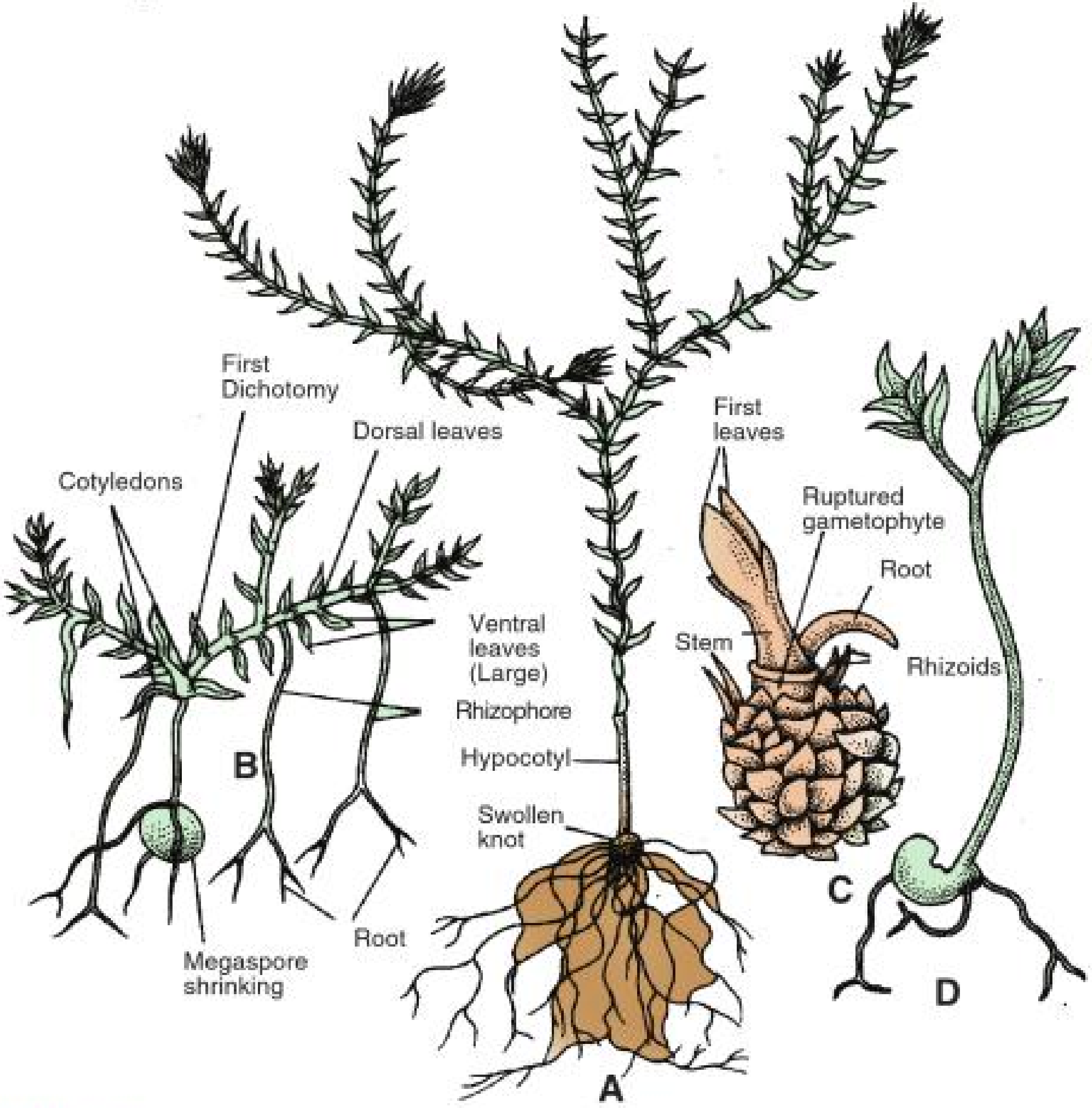

First Dichotomy
Dorsal leaves
Cotyledons
Ventral leaves (Large)
Rhizophore
B
Hypocotyl
Swollen knot
Root
Megaspore shrinking
A
First leaves
Ruptured gametophyte
Root
Stem
Rhizoids
C
D

Fig. 6.2 (A—D). *Selaginella* A. Young plant of *S. selaginoides*; B. Young plant of *S. kraussiana*; C—D. Young sporophytes of *S. kraussiana*.

Leaves

The leaves are microphyllous. Each leaf is traversed by a single unbranched midrib. The leaf traces do not leave any leaf gaps in the stem stele. A ligule arises from the base of each leaf (ligulate). They are delicate, green, with entire or serrate margin and acute apex. In xerophytic species the leaves are rough and thick. They are variegated in ***S. picta.*** Mostly the leaves are glabrous but hairy in ***S. hispida*** and some other species. A periodic change in leaf colour occurs in ***S. serpens.***

The leaves are sessile and may be ovate, linear, lanceolate or cordate. Abnormal pinnatifid leaves have been reported in ***S. lyallii*** (Bruchmann, 1909).

There are about fifty species of ***Selaginella*** in which the leaves in a plant are all of one kind. Such a condition is called **isophylly** and the leaves are called **isophyllous.** They are included in section **Homoeophyllum.** The leaves in majority of species are of two kinds, ***i.e.***, small and large (Fig. 6.1, B). Such a condition is called **anisophylly** and the leaves are called **anisophyllous** or dimorphic (section **Heterophyllum**).

The phyllotaxy or the arrangement of the leaves on the stem is always spiral in the isophyllous species of Selaginella (Fig. 6.2, A).

In the anisophyllous species of ***Selaginella e.g.***, ***S. chrysocaulos*** (Fig. 6.1, A), the small and large leaves form four longitudinal rows. The smaller leaves are arranged in two rows along the dorsal side of the stem. The larger leaves on the ventral side have their dorsal side turned towards the sky, whereas the small dorsal leaves have their ventral side facing the sky. The phyllotaxy is essentially decussate in all the dorsiventral ***Selaginellas***. A large ventral leaf is always opposite the small dorsal leaf so that the leaf pairs are unequal.

In some species of ***Selaginella e.g. S. grandis*** which grows erect, the main shoots, which may grow upto two to three feet in height, bear isophyllous leaves, whereas some of branches that arise from them bear anisophyllous leaves.

Ligule

The ligule develops quite early during the ontogeny of the leaf and arises from its base on the upper side. It varies in shape in different species of the genus. The ligule may be tongueshaped (***S. chrysocaulos***), wedge-shaped (***S. martensii***), lobed (***S. caulescens***), lanceolate or may even have fringed margins (***S. cuspidata***). A mature ligule has a prominent basal portion called the **glossopodium** (Fig. 6.8, F). The **glossopodium** is sunk in a definite ligular pit or pocket. Its function is not well understood. According to a number of workers the ligule is a secretory structure, which secretes or exudes water and sometimes mucilage and keeps the sporangium and the young leaf moist. The ligule during their development overgrow the leaf primordium and may be regarded as protective structures. They also overgrow the young sporangium.

Rhizophore

It is a structure of controversial morphological nature and present in most of the dorsiventral ***Selaginellas***. They are leafless and positively geotropic organs that have usually a localised origin and develop from the **angle meristems**, which are groups of meristematic cells present between the two branches of the stem. In majority of species only one rhizophore arises from an angle meristem but in ***S. martensii*** two rhizophores arise from such a meristem. One of them is ventral in position and the other dorsal. The latter remains short whereas the ventral one grows down into the soil and bears roots at its swollen end. In the climbing species the tips of rhizophores develop pad-like thickening and help in climbing.

In ***S. selaginoides*** and other radial species the rhizophores are absent.

Morphology of the rhizophore

Three different types of morphological interpretations have been advanced to solve the morphological nature of the rhizophore. According to one view they have been regarded as modified stems that bear adventitious roots (Pfeffier, Treub, Bruchmann, Velenovsky, Worsdell, Troll, Schoute).

The supporters of the second view (Harvey-Gibson, Van-Tiegham, Uphoff) regard them as roots. Bower and Goebel consider the rhizophores as organs ***sui generis*** (neither roots nor shoots).

The rhizophores are regarded as root-like structures due to the following characters : 1. They are positively geotropic. 2. They bear no leaves. 3. Their internal structure resembles that of a root. 4. Their stelar organisation is always monostelic even if the stems are polystelic.

Webster and Steeves (1964) and Bierhorst (1971) have almost discarded the term "rhizophore" and consider it to be a root. Bierhorst regards this term as of only historical interest. According to him such stem-like features are also known in the well established roots of other taxa. It is now known (Webster and Steeves, 1964) that the tip of the rhizophore divides to form roots, and the older belief that roots arise endogenously from tip of rhizophore is not valid. These observations rule out any difference between the root and the rhizophore. Exogenous roots are also known in some angiosperms.

The stem-like characteristics of rhizophores are : 1. Their exogenous origin (roots of some angiosperms, ***e.g.***, ***Nasturtium austriacum*** arise exogenously from the stem). 2. They develop from special meristems called the angle meristems that are present between the two branches of the stem. 3. They lack root caps (capless roots are also known). 4. They have no root hair. 5. Experimental evidence that under certain experimental conditions the rhizophores develop into leaf-bearing shoots.

J.C. Schoute (1938) regards them as stem with root-bearing functions because they lack root caps and root hair and are exogenous in origin. Regarding its anatomy. Schoute points out that it is like stem in its organisation.

It has been experimentally demonstrated by Bruchmann (1905) in ***S. kraussiana*** and by Williams (1931, 1937) in ***S. grandis*** and ***S. martensii*** that cessation of vegetative activity by inducing strobili formation or by decapitating leaf-bearing shoots, the rhizophore rudiments can be made to grow into leafy shoots. Cusik (1954) concluded that some hormones produced by shoot apex induce angle meristems to grow into rhizophores. He proved it experimentally.

After these experimental evidences, Williams and others did not decide to regard the rhizophores as transformed shoots but agreed with Bower and Goebel in treating them as organs ***sui generis***. The term organs ***sui generis*** in this case implies that rhizophores are neither roots nor stems but are intermediate structures. According to Schoute an organ ***sui generis*** is the one that is a novelty and has not risen as a result of metamorphosis of any organ. He disagrees with Bower and others in regarding rhizophores as structure ***sui generis*** because they are not novel structures and possess features in common with both the stems and the roots.

S. umbrosa

S. braunii

Roots

The roots are adventitious and originate from the (***i***) tips of rhizophores, (ii) from the swollen bases of hypocotyl and (iii) directly from the stem. They arise endogenously and branch dichotomously. In ***S. chrysocaulos*** and other dorsiventral species they arise from the swollen tips of the rhizophores. In ***S. selaginoides*** they arise from the swollen bases of the hypocotyl (Fig. 6.2, A). In ***S. umbrosa***, ***S. braunii***, etc., they arise directly from the stem and have no relation to the branching ***i.e.,*** they can arise from anywhere all along the stem. In some cases the roots arise only from the places where the stems branch ***e.g.***, ***S. densa.***

The roots have root caps and bear root hair. In ***S. selaginoides*** an endophytic fungus has been reported in the cortical cells of the root.

ORGANIZATION OF THE STROBILUS

The strobilus (Fig. 6.3, A.B) is the sporangia-bearing region of the sporophyte. The sporangia arise in the axils of leaves called the **sporophylls.** The sporophylls are like ordinary vegetative leaves but may differ in shape and size. There are two kinds of sporangia in ***Selaginella*** : (***i***) the **microsporangia** and (***ii***) the **megasporangia.** The sporophylls bearing microsporangia may be called the **microsporophylls** and those bearing megasporangia as **megasporophylls.** There is no morphological or anatomical differentiation between the micro and the megasporophylls. The **strobilus** is always terminal in position. Its formation usually results in the cessation of apical growth. In some cases, however, the axis of the strobilus resumes growth, ***i.e.***, it poliferates and overgrows the strobilus to form a normal dorsiventral shoot, ***e.g.***, ***S. grandis.*** In ***S. erythropus*** the proliferating strobilus produces a sterile shoot which again bears another strobilus at its tip. Such a condition results in the formation of two strobili on the same branch.

In ***Selaginella selaginoides*** the storobilus is cylindrical. The sporophylls are spirally arranged and are isophyllous. It is clearly marked off from the vegetative region. In ***S. molliceps*** sporangia have also been found to develop in the axils of ordinary vegetative leaves. In a large number of species the strobilus is tetragonous or four-angled. The sporophylls in the tetragonous strobilus may be isophyllous or anisophyllous and may be spirally arranged or decussate. In ***S. pallidissima***, ***S. chrysocaulos***, ***S. chrysorrhizos***, etc., the vegetative region as well as the strobili (tetragonous) are anisophyllous. In all these cases the sporophylls are ligulate and the ligule is present between the sporangium and the base of the sporophylls.

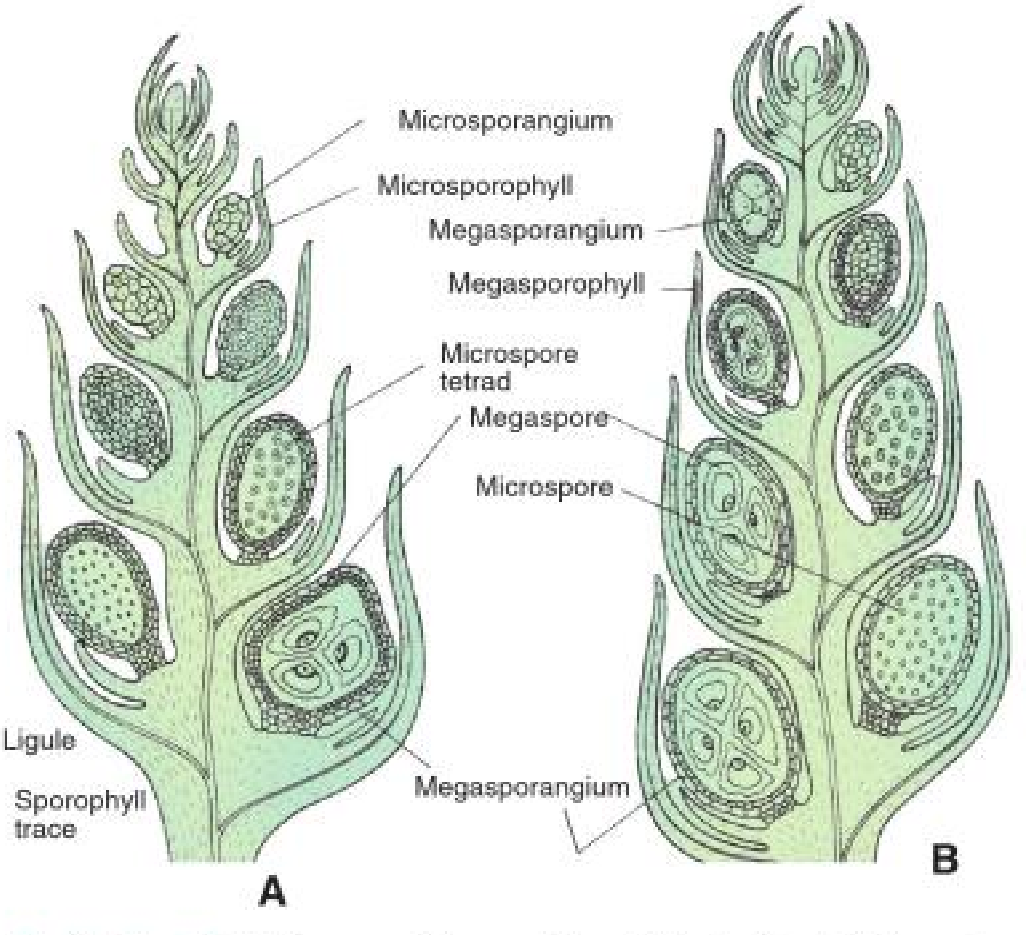


Fig. 6.3 (A—B). V. S. sporangiferous spikes of *Selaginella*. **A.** S. *kraussiana*; **B.** S. *oregana*.

The strobilus is also called the **sporangiferous spike** or the **cone.** Each sporophyll bears one sporangium in its axil (**axillary**) or a little upwards on the stem (**cauline**). The strobili are usually bisporangiate, *i.e.*, they bear both micro-and megasporangia in the axils of the respective sporo phylls. Such strobili are protandrous. The two kinds of sporophylls have no fixed position on the strobilus and they are variously positioned in different species of the genus. In ***S. chrysocaulos***, ***S. rupestris*** and many others the megasporophylls are restricted to the base of the strobilus and the microsporophylls to the upper region. In ***S. caulescens*** and ***S. martensii*** the two kinds of sporophylls are indiscriminately mingled along the entire length of the strobilus. In ***S. kraussiana*** (Fig. 6.3, A) there is only one megasporophyll at the base of the strobilus and the rest are all microsporophylls. In ***S. oregana*** (Fig. 6.3, B) the tetragonous stobilus has two rows of microsporophylls on one side and two rows of megasporophylls on the other side.

In ***S. atroviridis*** and ***S. gracilis*** the strobili are unisporangiate, ***i.e.***, a strobilus either bears microsporangia or it bears only megasporangia. Both the microsporangiate and megasporangiate strobili occur on the same plant.

ANATOMY

Stem

The vascular region or the ***stelar system*** in ***Selaginella*** exhibits considerable variation in the different species or even in different parts of the stem in the same species. Anatomy of ***S. chrysocaulos*** is given in detail. Variations in other species are, however, given in brief.

Selaginella chrysocaulos (Fig. 6.4, A).

It is a dorsiventral species and transverse section of a typical stem reveals the following structure :—

Epidermis

It is made up of a single layer of thin-walled rectangular or barrel-shaped cells and is covered by a thin layer of cuticle. The cells are colourless. There are no stomata.

Cortex

It consists of many layers of cells. The outermost layers (usually 2 to 4) of cells develop thick walls in the older regions of stem and form a **sclerenchymatous hypodermis.** The rest of the cortex is made up of thin-walled chlorenchymatous and polygonal cells. They enclose small intercellular spaces. In ***S. lepidophylla*** most of the cortex is sclerenchymatous. Sclerenchymatous hypodermis is absent in the younger parts of the stem in ***S. chrysocaulos***.

Air space

Next to the cortex there is large air space in the centre of which lies the stele suspended by means of **trabeculae.** The trabeculae are modified endodermal cells and possess casparian strips (Fig. 6.4, A). These trabeculae are actually cells of an endodermal layer. During the course of development (Fig. 6.4, C—E) the endodermal cells elongate radially (Fig. 6.4, D). As a result of this elongation the cells separate from each other (Fig. 6.4, D) and lead to the formation of air spaces. Further elongation results in the formation of a large air space traversed by elongated endodermal cells or the **trabeculae.** The trabeculae possess casparian strips. During the course of their radial elongation the trabeculae may divide and become two or more celled filaments.

Stele or the Vascular region

There is single central stele suspended in the air space by means of the trabeculae (Fig. 6.4, A). The stele in this species is flattened like a ribbon and is called a **protostele** because there is no pith in the centre. It consists of :—

(*a*) A single layer of thin-walled cells called the **pericycle.** The pericycle completely encircles the inner vascular tissues.

(*b*) Next to the pericycle is **phloem.** The phloem consists of a layer of phloem parenchyma cells next to the pericycle and a layer or two of **sieve cells.** The companion cells are absent. Phloem completely encircles the central xylem. The sieve cells appear as large polygonal cells in a cross section.

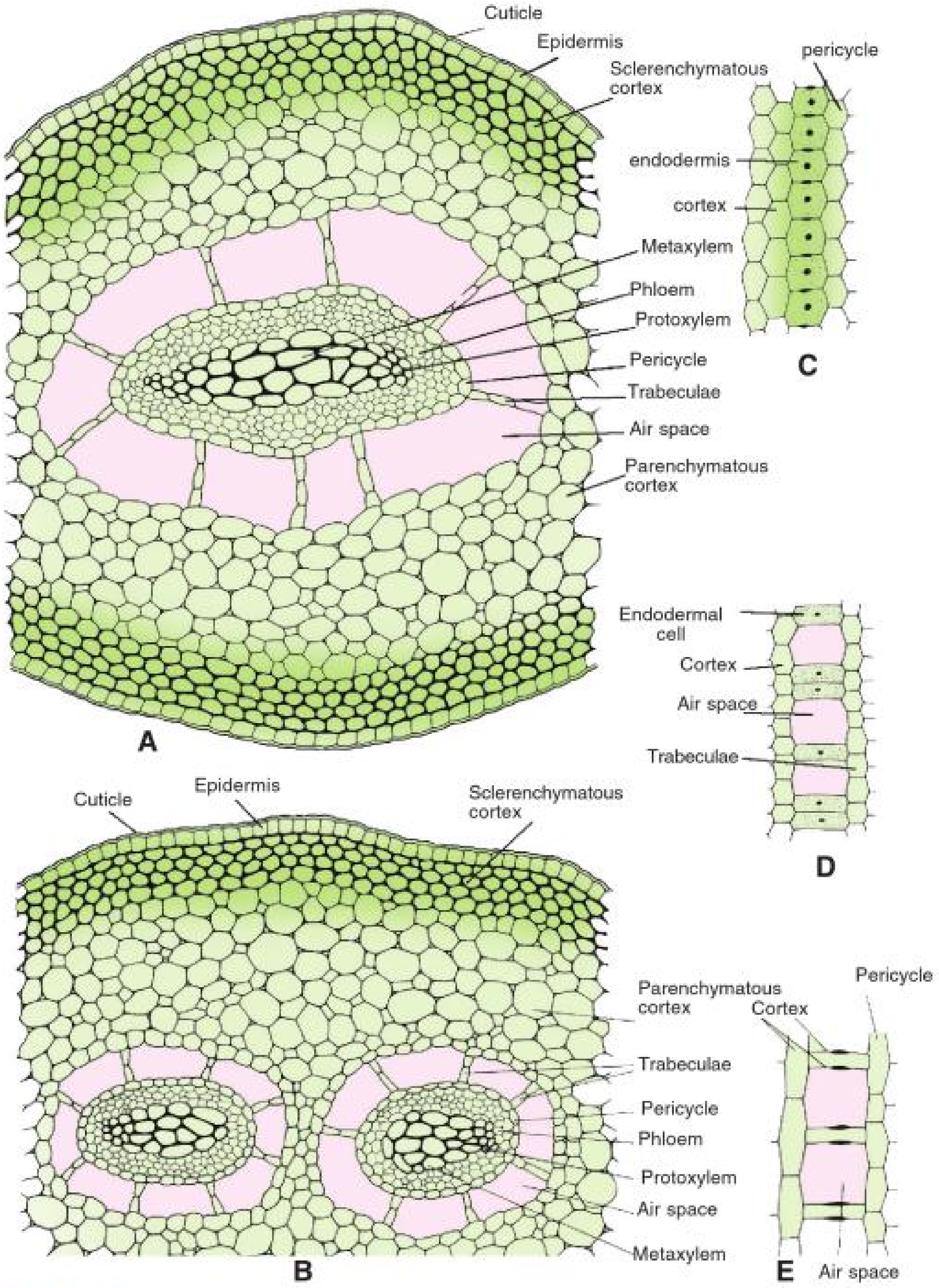
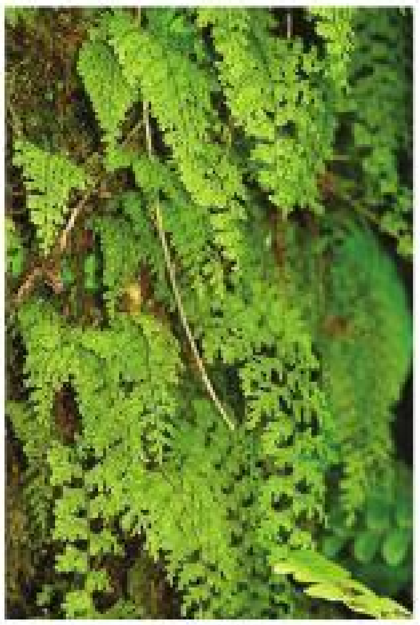

Cuticle
Epidermis
Sclerenchymatous cortex
pericycle
endodermis
cortex
Metaxylem
Phloem
Protoxylem
Pericycle
Trabeculae
Air space
Parenchymatous cortex
C
Endodermal cell
Cortex
Air space
Trabeculae
A
D
Cuticle
Epidermis
Sclerenchymatous cortex
Parenchymatous cortex
Pericycle
Cortex
Trabeculae
Pericycle
Phloem
Protoxylem
Air space
Metaxylem
B
E
Air space

Fig. 6.4. (A—E). **Anatomy of *Selaginella*. A.** T.S. stem of ***S. chrysocaulos*; B.** T.S. stem of ***S. kraussiana*.** Note distelic condition; C—E. Development of trabeculae.

(*c*) The centre of the stele is occupied by the xylem tissue. The xylem, therefore, forms the core of the stele, there being no pith. The xylem consists of **metaxylem** and **protoxylem.** The metaxylem is composed of scalariform tracheids and xylem parenchyma cells. It forms the major portion of the flattened stele. The protoxylem occupies the two ends of the flattened metaxylem and is composed of annular and spiral tracheids. The xylem is, therefore, **exarch**. Since there are two groups of protoxylem at either end, the xylem is regarded as **diarch**. The xylem lacks vessels and fibres.



S. flabellata

The protostele is **monostelic** because the stem has only one such stele. Other species with such a stele are ***S. martensii***, ***S. chrysorrhizos***, ***S. flabellata***, etc.

In ***S. selaginoides*** a section of the stem from the upper region of the axis reveals an **actinostelic** (star-shaped) **protostele** with 7 groups of exarch-proto-xylem. A cross section through a portion of the stem in trailing region reveals a monostelic protostele with mesarch xylem. In this case protoxylem is in the centre and is surrounded on all sides by metaxylem. In ***S. kraussiana*** there are two protosteles suspended in the air space. They are exarch. Such a stele is called distelic (Fig. 6.4, B).

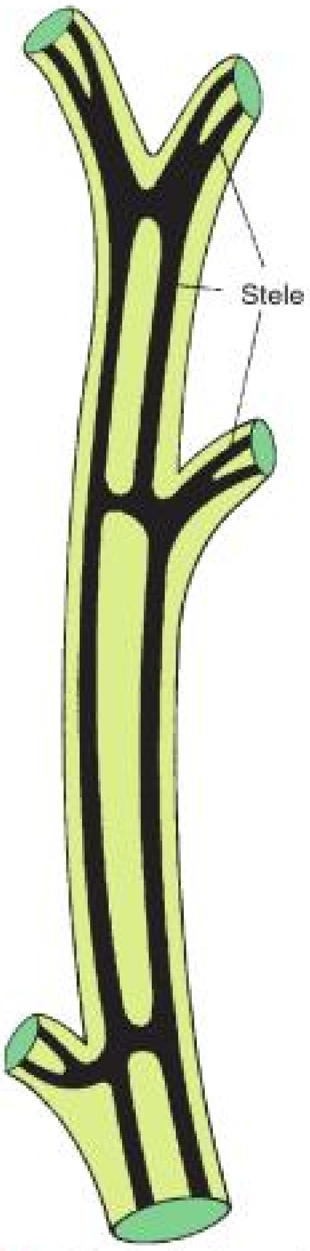


Fig. 6.5. ***Selaginella kraussiana.*** It shows longitudinal course of the two steles. They anastomose at the point of bifurcation of the stem.

The entire stem is traversed by two parallel steles that join only at the point of branching of the stem (Fig. 6.5) and again separate. Metaxylem consists of scalariform tracheids, whereas protoxylem is composed of annular and spiral tracheids. Bierhorst (1960) and Zamora (1960) reported that the helics of spiral tracheids in this species are variously wound in different parts of the same tracheid. The xylem is encircled by phloem which in turn is surrounded by pericycle. The phloem consists of a single layer of sieve cells and parenchyma cells. Esau (1953), and Cheadle and Gifford (1953), reported that the sieve cells have many sieve areas on their inclined end walls and lateral walls. ***Selaginella sulcata***, ***S. galeottei***, ***S. willdenovii***, etc., belong to this category.

Selaginella sulcata

In ***S. willdenovii*** (Fig. 6.6) there are three or even four ribbon-like protosteles. The xylem is exarch. There are two groups of protoxylem, one at either end, in the central stele whereas in the other two that lie on either side of it there are more than two groups of protoxylem (Fig. 6.6). The xylem is

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.

You have either reached a page that is unavailable for viewing or reached your viewing limit for this book.